

# Small games and long memories promote cooperation

Alexander J. Stewart<sup>1,2</sup>, Joshua B. Plotkin<sup>1</sup>

<sup>1</sup> Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

<sup>2</sup> Current address: Department of Genetics, Environment and Evolution, University College London, London, UK

Complex social behaviors lie at the heart of many of the challenges facing evolutionary biology, sociology, economics, and beyond. For evolutionary biologists in particular the question is often how such behaviors can arise *de novo* in a simple evolving system. How can group behaviors such as collective action, or decision making that accounts for memories of past experience, emerge and persist? Evolutionary game theory provides a framework for formalizing these questions and admitting them to rigorous study. Here we develop such a framework to study the evolution of sustained collective action in multi-player public-goods games, in which players have arbitrarily long memories of prior rounds of play and can react to their experience in an arbitrary way. To study this problem we construct a coordinate system for memory- $m$  strategies in iterated  $n$ -player games that permits us to characterize all the cooperative strategies that resist invasion by any mutant strategy, and thus stabilize cooperative behavior. We show that while larger games inevitably make cooperation harder to evolve, there nevertheless always exists a positive volume of strategies that stabilize cooperation provided the population size is large enough. We also show that, when games are small, longer-memory strategies make cooperation easier to evolve, by increasing the number of ways to stabilize cooperation. Finally we explore the co-evolution of behavior and memory capacity, and we find that longer-memory strategies tend to evolve in small games, which in turn drives the evolution of cooperation even when the benefits for cooperation are low.

Behavioral complexity is a pervasive feature of organisms that engage in social interactions. Rather than making the same choices all the time – always cooperate, or never cooperate – organisms behave differently depending on their social environment or their past experience. The need to understand behavioral complexity is at the heart of many important challenges facing evolutionary biology as well as the social sciences, or indeed any problem in which social interactions play a part. Cooperative social interactions in particular play a central role in many of the major evolutionary transitions, from the emergence of multi-cellular life to the development of human language [1].

Evolutionary biologists have been successful in pinpointing biological and environmental factors that influence the emergence of cooperation in a population. The demographic and spatial structure of populations in particular have emerged as fundamentally important factors [2–8]. At the other end of the scale, the underlying mechanisms of cooperation – such as the genetic architectures that encode social traits, or the ability of public goods to diffuse in the environment – also place constraints on how and to what extent cooperation will evolve [9–13].

Despite extensive progress for simple interactions, an understanding of the evolution of cooperation when social interactions occur repeatedly – so that individuals can update their behavior in the light of past experience – and involve multiple participants simultaneously, remains elusive. Some of the most promising approaches for tackling this problem come from the study of iterated games [1, 2, 14–17, 20, 21]. In the language of game theory, behavioural updates in light of past experience are modelled as a strategy in an iterated multi-player game among heterogeneous individuals. Even when we limit ourselves to a small

set of relatively simple strategies in such games, the resulting evolutionary dynamics are often surprising and counter-intuitive. As we begin to allow for a wider array of ever more complex behaviors, results on the emergence of cooperation are correspondingly harder to pin down.

In this paper we study evolving populations composed of individuals playing arbitrary strategies in iterated, multiplayer games. We focus on the prospects for cooperation in public-goods games, and we investigate how these prospects depend on the number of players that simultaneously participate in the game, on the memory capacity of the players, and on the total population size. We then study the co-evolution of players' strategies alongside their capacity to remember prior interactions. We arrive at a simple insight: when games involve few players, longer memory strategies tend to evolve, which in turn increases the amount of cooperation that can persist. And so populations tend to progress from short memories and selfish behavior to long memories and cooperation.

## 1 Results

We study the evolution of cooperation in iterated public-goods games, in which  $n$  players repeatedly choose whether to cooperate by contributing a cost  $C$  to a public pool, producing a public benefit  $B > C$ . In each round of iterated play the total benefit produced due to all player's contributions is divided equally between all players. Thus, if  $k$  players choose to cooperate in a given round, each player receives a benefit  $Bk/n$ . We study finite populations of  $N$  players engaging in infinitely iterated  $n$ -player public-goods games, using strategies with memory length  $m$ , meaning a player can remember how many times she and her opponents cooperated across the preceding  $m$  rounds (Figure 1).

We focus on the evolution of sustained collective action, meaning the evolution of strategies that, when used by each member of the population, produce an equilibrium play with all players cooperating each round. This may be thought of as the best possible social outcome of the game, because it produces the maximum total public good. We contrast the prospects for sustained cooperation with the prospects for sustained *inaction*, meaning strategies that, when used by each member of the population, produce an equilibrium play with all players defecting each round. This may be thought of as the worst possible social outcome of the game, because it results in no public good being produced at all.

To study the evolutionary prospects of collective action and inaction we determine the “volume of robust strategies” that produce sustained cooperation or defection in a repeated  $n$ -player game, in which players have memory  $m$ . The game is played in a well-mixed population, composed of  $N$  haploid individuals who reproduce according to a “copying process” based on their payoffs (Figure 1) [7]. The volume of robust strategies measures how much cooperation or defection will evolve across many generations [3]. More specifically, this volume is the probability that a randomly drawn strategy that produces sustained cooperation (or defection) can resist invasion by all other possible strategies that do not produce sustained cooperation (or defection) [2, 3, 8, 25, 26]. As we have shown previously [3], the volumes of robust strategies determine the evolutionary dynamics of cooperation and defection in iterated games. We confirm the utility of this approach by comparing our analytical predictions to Monte Carlo simulations, studying the effects of population size, game size, and memory capacity on the evolution of cooperation.

We begin our analysis by describing a coordinate system under which the volume of robust strategies can be determined analytically, for games of size  $n$ , played in populations of size  $N$ , in which strategies have memory length  $m$ . We use this coordinate system to completely characterize all evolutionary robust cooperating (and defecting) strategies, which cannot be invaded by any non-cooperating (or non-defecting) mutants, in the iterated  $n$ -player public-goods game. We apply these results to make specific predictions for the effects of game size and of memory capacity on the evolution of collective action through sustained cooperation. Finally we explore the consequences of these predictions for the co-evolution of cooperation and memory capacity itself.

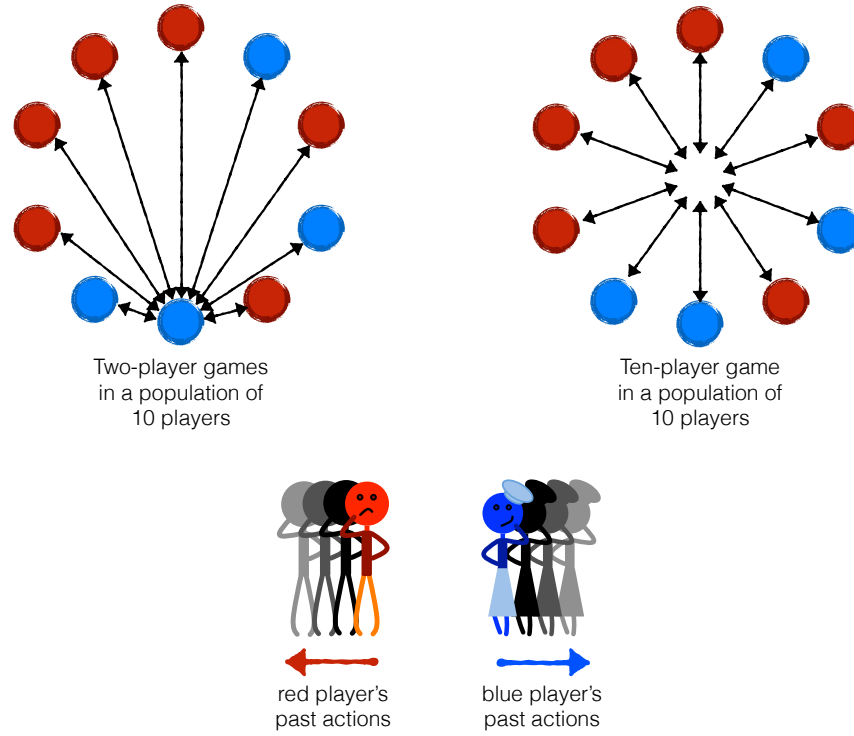


Figure 1: Multiplayer games and memory. We study the evolution of behavior in iterated  $n$ -player public-goods games in which players use strategies with memory capacity  $m$ . We consider a replicating population of  $N$  individuals who each receive a payoff from engaging in an infinitely iterated game with all possible subsets of  $(n - 1)$  opponents in the population. Players then reproduce according to a “copying process”, in which a player  $X$  copies another player’s strategy  $Y$  with a probability  $f_{X \rightarrow Y} = \frac{1}{1 + \exp[\sigma(S^X - S^Y)]}$  where  $S^X$  and  $S^Y$  are the player’s respective payoffs and  $\sigma$  scales the strength of selection. We consider the case of strong selection, such that a rare mutant who is at a selective disadvantage is quickly lost from the population [3]. We investigate the success of cooperative strategies as a function of game size and the length of players’ memories. We determine the frequency of robust cooperative strategies, which can resist invasion by any possible mutant. (Top) Depending on the size of the game  $n$  relative to the population  $N$ , the dynamics of public-goods games are different. In a two-player game, a series of pairwise interactions occur in the population at each generation (left). If the whole population plays the game each generation (right) all players interact simultaneously. (Bottom) Memory of past events results in strategies that update behavior depending on the histories of both players’ actions. This allows for more complex strategies, such as those that punish rare defection or reward rare cooperation.

### 1.1 Beyond two-player games and memory-1 strategies

Recently, Press and Dyson introduced so-called zero determinant (ZD) strategies in iterated two-player games [1]. ZD strategies are of interest because, when a player unilaterally adopts such a strategy she enforces a linear relationship between her longterm payoff and that of her opponent, and thereby gains some measure of control over the outcome of the game [27–31]. Several authors have worked to extend the framework of Press and Dyson to multi-player games [29, 32] and have characterized multi-player ZD strategies, revealing a number of interesting properties.

Other research has expanded the framework of Press and Dyson to study all possible memory-1 strategies for infinitely repeated, two-player games [2, 3, 8, 25, 26]. This work involves developing a coordinate

system for the space of all memory-1 strategies [2] that allows us to describe a straightforward (although not necessarily linear) relationship between the two players' longterm payoffs. This relationship between players' longterm payoffs, in turn, has enabled us to fully characterize all memory-1 Nash equilibria and all evolutionary robust strategies for infinitely repeated two-player games, played in a replicating population of  $N$  individuals [2, 3, 8, 26].

Here we generalize this body of work by developing a coordinate system for the space of memory- $m$  strategies in multi-player games of size  $n$ , such that all  $n$  players' longterm payoffs are related in a straightforward (although not necessarily linear) way. One essential trick that enables us to achieve this goal is to construct a mapping between memory- $m$  strategies in an  $n$ -player game and memory-1 strategies in an associated  $n \times m$ -player game. We then construct a coordinate system for the space of memory-1 strategies in multi-player games that allows us to easily characterize the cooperating and the defecting strategies that resist invasion. We apply these techniques to the case of iterated  $n$ -player public-goods games and we precisely characterize all evolutionary robust memory- $m$  strategies – i.e. those strategies that, when resident in a finite population of  $N$  players, can resist selective invasion by all other possible strategies – thereby elucidating the prospects for the evolution of cooperation in a very general setting.

## 1.2 A coordinate system for long-memory strategies in multi-player games

Our goal is to study the effects of game size and memory on the frequency and nature of collective action in public-goods games. Allowing for long-memory strategies and games with more than two players greatly expands the potential for behavioral complexity, because players are able to react to the behaviors of multiple opponents across multiple prior interactions. And so merely determining the payoffs received by players in such an iterated public-goods game can pose a significant challenge. In order to tackle this problem we develop a coordinate system for parameterizing strategies, in which the outcome of a game between multiple players using long-memory strategies can nonetheless be easily understood.

A player using a memory- $m$  strategy chooses her play in each round of an iterated game in a way that depends on the history of plays by all  $n$  players across the preceding  $m$  rounds. In general such a strategy consists of  $2^{n \times m}$  probabilities for cooperation in the present round. We write the probability for cooperation of a focal player in its most general form as  $p_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}} \in [0, 1]$  where  $\sigma_i$  denotes the history of plays for player  $i$ . Each  $\sigma_i$  corresponds to an ordered sequence of  $m$  plays for player  $i$ , with each entry taking the value **c** (cooperate) or **d** (defect). The  $2^{n \times m}$  probabilities for cooperation form a basis for  $\mathbb{R}^{2^{n \times m}}$  and constitute a system of coordinates for the space of memory- $m$  strategies in  $n$ -player games. In the supporting information we describe in detail how to construct of an alternate coordinate system of  $2^{n \times m}$  vectors that also form a basis for  $\mathbb{R}^{2^{n \times m}}$ , and which greatly simplifies the analysis of long-term payoffs in iterated games. Below we describe this alternative coordinate system for the specific case of iterated public-goods games, which are the focus of this study.

**(i) Mapping memory- $m$  to memory-1:** In order to simplify our analysis of long-memory strategies we will conceive of a focal player using a memory- $m$  strategy in an  $n$ -player game as a player who instead uses a memory-1 strategy in an associated  $n \times m$ -player game. That is, we will think of an  $n$ -player game in which a focal player uses a memory- $m$  strategy in terms of an equivalent  $n \times m$ -player game, which is composed of  $n$  “real” players along with  $m - 1$  “shadow” players associated with each real player. The shadow players play the same way that their associated real player did  $t$  rounds previously, for  $2 \leq t \leq m$ . The focal player's memory- $m$  strategy is thus identical to a memory-1 strategy in the  $n \times m$  player game, where the corresponding memory-1 strategy responds to a large set of “shadow” players whose actions in the immediately previous round simply encode the actions taken by the  $n$  real players in the preceding  $m$  rounds. This trick allows us to reduce the problem of studying long-memory strategies to the problem of studying memory-1 strategies, albeit with a larger number of players in the game.

All that is required is to construct strategies for the shadow players so that the state of the system across the preceding  $m$  rounds is correctly recreated at each round of the associated  $n \times m$ -player game.

This construction is straight forward. If the focal player played  $c$  in the last round, then we stipulate that her first shadow player will play  $c$  in the next round (i.e. it will copy her last move). Similarly her second shadow player will copy the last move of her first shadow player, and so on, up to her  $(m - 1)$ st shadow player. The same goes for the shadow players of each of her  $n - 1$  opponents. In this way, all the plays of the last  $m$  rounds in the  $n$ -player game are encoded at each round in the associated  $n \times m$ -player game.

Having transformed an arbitrary memory- $m$  strategy in an  $n$ -player into an associated memory-1 strategy in an  $n \times m$ -player game, we now describe a coordinate system for memory-1 strategies that allows us to derive a simple relation among the equilibrium payoffs to all players. We define this coordinate system for arbitrary games in the supporting information (section 3), and for the case of public-goods games below.

**(ii) Parameterizing strategies in public-goods games:** Under a public-goods game, a player who cooperates along with  $k$  of her opponents receives a net payoff  $Bk/n - C$ , whereas a player who defects while  $k$  of her opponents cooperate receives a net payoff  $Bk/n$ . That is, the payoff received depends on whether or not the focal player cooperated and on the number of her opponents that cooperated, but it does not depend on the identity of her cooperating opponents. Likewise, if a player has memory of the preceding  $m$  rounds of an iterated public-goods game, then her payoff across those rounds depends on the total number of times she cooperated and the total number of times her opponents cooperated, but it does not depend on the order in which different players cooperated nor on the identity of her cooperating opponents. Therefore, rather than studying the full space of  $2^{n \times m}$  probabilities for cooperation, we can limit our analysis for iterated public-goods games to strategies that keep track of the total number of times a focal player cooperated, and the number of times her opponents cooperated, within her memory capacity. A focal player's strategy can thus be expressed as  $((n - 1)m + 1) \times (m + 1)$  probabilities for cooperation each round,  $p^{l_o, l_p}$ , where  $l_o$  denotes the total of number of times the player's opponents cooperated in the preceding  $m$  rounds (which number can vary between 0 and  $(n - 1)m$ ) and  $l_p$  denotes the total number of times the player herself cooperated in the preceding  $m$  rounds (which can vary between 0 and  $m$ ).

Although the probabilities  $p^{l_o, l_p}$  are perhaps the most natural coordinates for describing a memory- $m$  strategy in an iterated  $n$ -player public-goods game, we have developed an alternative coordinate system, defined in Figure 2, that simplifies the analysis of equilibrium payoffs and the evolutionary robustness of strategies. The alternative system of  $((n - 1)m + 1) \times (m + 1)$  coordinates for a given player's strategy is described by parameters  $\{\chi, \phi, \kappa, \Lambda^{0,0}, \dots, \Lambda^{(n-1) \times m, m}\}$  defined in Figure 2. We impose the boundary conditions  $\Lambda^{0,0} = \Lambda^{(n-1) \times m, m} = 0$  along with one other linear relationship on the  $\Lambda$  terms (see supporting information). Qualitatively, this coordinate system describes the probability of cooperation in a given round,  $p^{l_o, l_p}$ , in terms of a weighted sum of five components: (1) The tendency to repeat past behavior; (2) The baseline tendency to cooperate ( $\kappa$ ); (3) The tendency to cooperate in proportion to the payoff received by the focal player ( $\chi$ ); (4) The tendency to punish (i.e. defect) in proportion to the payoffs received by her opponents ( $\phi$ ) and (5) The tendency to punish in response to the specific outcome of the previous rounds ( $\Lambda^{l_o, l_p}$ ).

The advantage of using this coordinate system is that it provides a simple relationship between the long-term payoff to a focal player 0,  $S^0$ , and the the long-term payoffs  $S^i$  of each of her opponents  $i$  in an iterated  $n$ -player public-goods game:

$$\phi \sum_{i=1}^{n-1} \frac{S^i}{n-1} - \chi S^0 - \kappa(\phi - \chi) + \sum_{l'_o=0}^{(n-1) \times m} \sum_{l'_p=0}^m \hat{\Lambda}^{l'_o, l'_p} w^{l'_o, l'_p} = 0. \quad (1)$$

Here the term  $w^{l'_o, l'_p}$  denotes the equilibrium rate at which the invading player cooperates  $l'_p$  times and his opponents cooperate  $l'_o$  times over the preceding  $m$  rounds, and  $\hat{\Lambda}^{l'_o, l'_p}$  denotes the contingent punishment of the focal strategy from the point of view of a mutant (see supporting information for a derivation of 1).

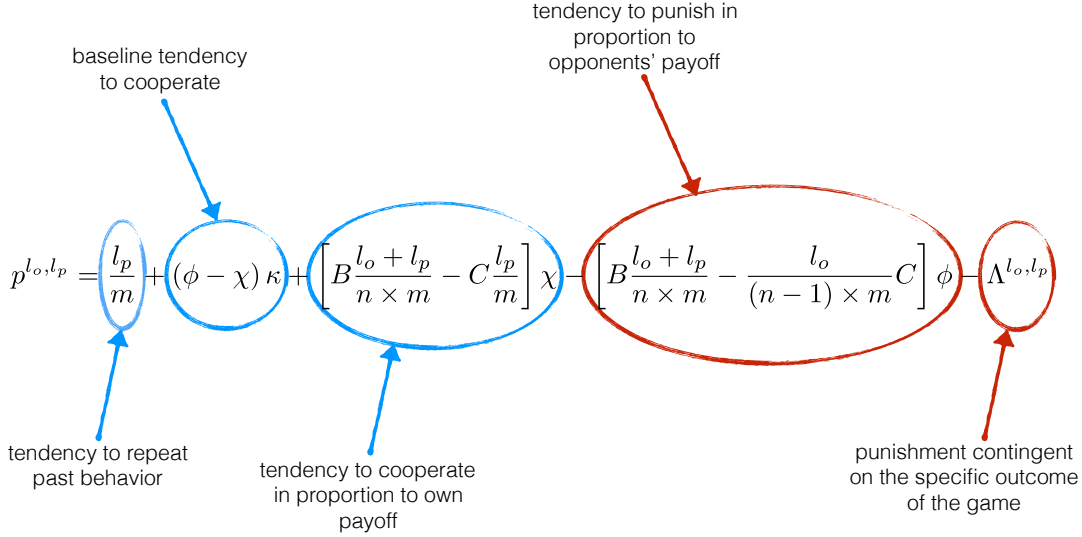


Figure 2: A co-ordinate system for describing strategies in public-goods games. We consider the space of strategies of the form  $p^{l_o, l_p}$ , such that players cooperate with a probability that depends on the number of times  $l_o$  her opponents have cooperated and the number of times  $l_p$  she has cooperated within her memory. We define the strategy of a focal player by coordinates  $\{\chi, \phi, \kappa, \Lambda^{0,0}, \dots, \Lambda^{(n-1) \times m, m}\}$  as shown in the figure. The components of this coordinate system have an intuitive interpretation: the probability that a player cooperates depends on (1) her past tendency to cooperate, (2) a baseline tendency to cooperate ( $\kappa$ ), (3) a tendency to cooperate in proportion to her own payoff ( $\chi$ ), (4) a tendency to punish (i.e. defect) in proportion to her opponents' payoffs ( $\phi$ ) and (5) a contingent punishment that depends on the specific outcome of the game over the prior  $m$  rounds ( $\Lambda^{(n-1) \times m, m}$ ).

$\hat{\Lambda}'^{l_o, l_p}$  is related in a simple way to the terms  $\Lambda^{l_o, l_p}$ , so that increasing  $\Lambda^{l_o, l_p}$  increases  $\hat{\Lambda}'^{l_o, l_p}$  (see supporting information).

### 1.3 The effects of game size on robust cooperation

The relationship among payoffs summarized in 1 provides extensive insight into the outcome of iterated public-goods games. Of particular interest are the prospects for cooperation as the game size  $n$  and population size  $N$  grow. Public-goods games are well known examples of the collective action problem, in which increasing the number of players in a game worsens the prospects for cooperation [33, 34]. Larger populations, on the other hand, tend to make it easier to evolve robust cooperation, at least for two-player games [8]. We will use 1 to explore the tradeoff between game size and population size, and the nature of robust cooperative behaviors that can evolve in multi-player games.

1 allows us to characterize the ability of a cooperative strategy to resist invasion by any other strategy in a population of size  $N$  [2, 3, 8, 26]. We define a cooperative strategy as one which, when played by every member of a population, assures that all players cooperate at equilibrium and thus receive the payoff for mutual cooperation,  $B - C$ . This implies the necessary condition  $p^{(n-1) \times m, m} = 1$ , so that if all players cooperated in the preceding  $m$  rounds, a player using a cooperative strategy is guaranteed to cooperate in the next round. We call such strategies “cooperators” meaning that they produce sustained cooperation when resident in a population. In the alternate coordinate system developed above a necessary condition for sustained cooperation is  $\kappa = B - C$ .

Conversely, we also consider strategies that lead to collective *inaction*, meaning sustained defection. Such strategies must have  $p^{0,0} = 0$ , which implies a necessary condition  $\kappa = 0$  in the alternate coordinate system. We call strategies satisfying this condition “defectors” meaning that they produce sustained defection when resident in a population.

A rare mutant  $i$  can invade a population of size  $N$  in which a cooperative strategy is resident only if he receives a payoff  $S^i$  that exceeds the payoff received by the resident cooperator. By considering bounds on the payoffs received by players (see supporting information) we have derived necessary and sufficient conditions for a cooperative strategy  $\{\chi, \phi, \kappa, \hat{\Lambda}^{0,0}, \dots, \hat{\Lambda}^{(n-1) \times m, m-1}\}$  to resist selective invasion by any mutant strategy – that is, for a cooperative strategy to be evolutionary robust:

$$\begin{aligned}
C_s^{n,m} &= \left\{ (\chi, \phi, \kappa, \hat{\Lambda}^{0,0}, \dots, \hat{\Lambda}^{(n-1) \times m, m-1}) \middle| \kappa = B - C, \right. \\
&\quad \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq \\
&\quad C \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}, \\
&\quad \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq \\
&\quad \left. (B-C) \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p} \right\}.
\end{aligned} \tag{2}$$

2 allows us to make a number of observations about the prospects and nature of robust cooperation. First, all other things being equal, larger values of  $\hat{\Lambda}^{l_o, l_p}$ , which correspond to stronger contingent punishment, in which players successfully punish rare defection, make it easier for a strategy to satisfy the requirements for robust cooperation. Second, positive values of  $\chi$ , corresponding to more generous strategies [8], in which players tend to share the benefits of mutual cooperation, also make it easier for a strategy to satisfy the requirements for robust cooperation. Thus, complex strategies that punish rare defection and are generous to other players tend to produce robust cooperative behavior in an evolving population.

2 also shows that larger values of  $n$ , corresponding to games with more players, tend to make for smaller volumes of robust cooperative strategies. This can be seen on the left-hand side of the inequality in 2, where increasing  $n$  attenuates the impact of contingent punishment on robustness. Likewise, this can also be seen on the right-hand side of the inequality in 2, where increasing  $n$  attenuates the impact of generosity on robustness.

The effects of game size on the prospects for cooperation can be illustrated by considering two extreme cases. When the entire population takes part in a single multi-player game, so that  $n = N$ , then 2 implies that strategies can be robust only if  $\chi \geq \phi$ . However, in order to produce a viable strategy  $\chi \leq \phi$  is required (Fig. 2); and so the only possible way to ensure robust cooperation in this extreme case is to have  $\chi = \phi$ . The condition  $\chi = \phi$  gives a tit-for-tat-like strategy, and it results in unstable cooperative behavior in the presence of noise [3]. And so, in the limit of games as large as the entire population size the prospects for evolutionary robust cooperation are slim. However, in the contrasting case in which the population size is much larger than the size of the game being played, that is  $N \gg n \gg 1$ , then 2 shows that a positive volume of robust cooperative strategies always exists, given sufficient contingent punishment  $\hat{\Lambda}^{l_o, l_p}$ , even in very large games.

Understanding the expected rate of cooperation in multi-player games requires that we compare the volume of robust cooperative strategies to the volume of robust defecting strategies. A rare mutant  $i$  can invade a population in which a defecting strategy is resident only if he receives a payoff  $S^i$  that exceeds the payoff received by the resident defector. The resulting necessary and sufficient conditions for the

robustness of defecting strategies are then:

$$\begin{aligned}
\mathcal{D}_s^{n,m} = & \left\{ (\chi, \phi, \kappa, \hat{\Lambda}^{0,0}, \dots, \hat{\Lambda}^{(n-1) \times m, m}) \middle| \kappa = 0, \right. \\
& \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq \\
& - (B - C) \left( \phi \frac{N(n-2) + 1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}, \\
& \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq \\
& \left. - C \left( \phi \frac{N(n-2) + 1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p} \right\}.
\end{aligned} \tag{3}$$

Once again, we see from 3 that larger values of  $\hat{\Lambda}^{l_o, l_p}$ , resulting in stronger contingent punishment of rare cooperators in a population of defectors, makes it easier for a defecting strategy to be robust. However, in contrast to the case for cooperators, *decreasing*  $\chi$ , which for defectors corresponds to more extortionate behavior, such that players try to increase their own payoff at their opponents' expense [1], makes a defecting strategy more likely to satisfy the requirements for robustness. Finally, while larger values of  $n$  attenuate the effect of contingent punishment on robustness, they also make more extortionate strategies more robust; and the latter effect is always stronger, so that larger games permit a greater volume of defecting strategies. In the extreme case of  $n = N$  all defecting strategies are robust. Overall, 3 implies that increasing game size  $n$  tends to increase the volume of robust defectors, in contrast to its effect on robust cooperators.

We confirmed our predictions for the effects of game size on the volume of robust cooperators and defectors by analytical calculation of robust volumes, from Eqs. 2-3, and by comparison to direct simulation for the invasibility of cooperators and defectors against a large range of mutant invaders (Figure 3a). As game size increases the volume of robust cooperators decreases relative to the volume of robust defectors, making cooperation harder to evolve.

There is a simple intuition for why larger games make cooperation less robust and defection more robust: In public-goods games with more players, the marginal change in payoff to a player who switches from cooperation to defection is  $C - B/n$ , and so the incentive to defect grows as the size of the game grows. This of course is the group size paradox, and it is a well known phenomenon for any collective action problem [33]. In the limiting case  $n = N$  the only hope for robust cooperation is tit-for-tat-like strategies, that are capable of both sustained cooperation and sustained defection, depending on their opponent's behavior.

In general, both cooperators and defectors have positive volumes of robust strategies, provided  $n < N$ . As such, both cooperation and defection can evolve. Although these robust strategies cannot be selectively invaded by any other strategy when resident in a population, they can be neutrally replaced by a non-robust strategy of the same type, which can in turn be selectively invaded. As a result, there is a constant turnover between cooperation and defection over the course of evolution, with the relative time spent at cooperation versus defection determined by their relative volumes of robust strategies [3, 26].

Our results show that the problem of collective action is alleviated by sufficiently large population sizes. That is, for an arbitrarily large game size  $n$  we can always find yet larger population sizes  $N$  such that robust cooperative strategies are guaranteed to exist. Moreover, increasing the population size  $N$  leads to increasing volumes of robust cooperative strategies and decreasing volumes of robust defecting strategies (Figure S1).



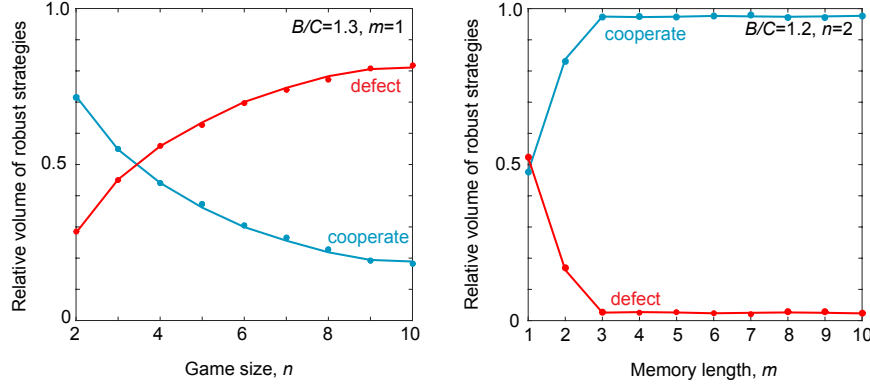


Figure 3: The impact of game size and memory capacity on cooperation. We calculated the relative volumes of robust cooperation – that is, the absolute volume of robust cooperative strategies divided by the total volume of robust cooperators and defectors – and compared this to the relative volume of defectors (solid lines) using Eqs. 2-3. We also verified these analytic results by randomly drawing  $10^6$  strategies and determining their success at resisting invasion from  $10^5$  random mutants (points). We calculated player’s payoffs by simulating  $2 \times 10^3$  rounds of a public-goods game. We then plotted the relative volumes of robust cooperators and robust defectors as a function of game size  $n$  (with fixed memory  $m = 1$ , left) and as a function of memory capacity  $m$  (with fixed game size  $n = 2$ , right). Increasing game size increases the relative volume of robust defection; while increasing memory length increases the relative volume of robust cooperation. In all calculations and simulations we used cost  $C = 1$  and benefit  $B$  as indicated in the figure.

#### 1.4 The effects of memory on robust cooperation

We have not yet said anything about the impact of memory capacity on the prospects for cooperation. Indeed, the robustness conditions Eqs. 2-3 do not depend explicitly on memory length  $m$ , as they do on game size  $n$  and on population size  $N$ . However, memory does have an important impact on the efficacy of contingent punishment,  $\hat{\Lambda}$ , on the left-hand sides of the inequalities in 2 and Eq. 3. Figure 3 illustrates the impact of increasing memory  $m$  on the volume of robust cooperative and robust defecting strategies. Here we see the opposite pattern to the effect for game size: as memory increases, there is a larger volume of robust cooperation relative to robust defection.

We can develop an intuitive understanding for the effect of memory on sustained cooperation by considering its role in producing effective punishment. A longer memory enables a player to punish opponents who seek to gain an advantage through rare deviations from the social norm: that is, rare defectors in a population of cooperators or rare cooperators in a population of defectors. However, using a long memory to punish rare defectors is a more effective way to enforce cooperation than punishing rare cooperators is to enforce defection (since in the latter case the default behavior is to defect anyway, and so increasing the amount of “punishment” has little overall effect on payoff). And so as memory increases, cooperators become more robust relative to defectors, as 2-3 and Figure 3 show.

The change in the efficacy of punishment for rare deviants from the social norm as memory capacity increases is illustrated in Figure S2, where we calculate the average  $\hat{\Lambda}^{l_o, l_p}$  for randomly-drawn cooperative or defecting strategies. We see that as memory capacity increases, a randomly drawn cooperator tends to engage in more effective punishment (larger values of  $\hat{\Lambda}^{l_o, l_o}$ ) whereas a randomly drawn defector tends to engage in less effective punishment (smaller values of  $\hat{\Lambda}^{l_o, l_o}$ ). This trend explains why increasing memory capacity increases the volume of robust cooperators relative to defectors.

## 1.5 Evolution of memory

Our results on the relationship between memory capacity and the robustness of cooperation raise a number of interesting questions. In particular, memory of the type we have considered does not seem to convey a direct advantage to cooperation (or defection), because a robust cooperative (or defecting) strategy is robust against *all possible invaders*, regardless of their memory capacity. However increased memory can nonetheless make robust cooperation easier to evolve, because it allows for more effective contingent punishment. This tends to have a stronger impact when games are small because, as described in Eqs. 2-3, the impact of contingent punishment on robustness is attenuated by a factor  $N - n$ , and thus the effect of longer memory on the contributions of  $\hat{\Lambda}$  terms to robust cooperation is smaller in larger games. And so, at least when the number of players is relatively small, we might expect long memories to facilitate the evolution of cooperation in populations.

What our analysis has not yet addressed is whether memory capacity itself can adapt, and what its co-evolution with strategies in a population will imply for the longterm prospects of cooperation. To address this question we undertook evolutionary simulations, allowing heritable mutations both to a player's strategy and also to her memory capacity. These simulations, illustrated in Figure 4, confirm that (i) longer memories do indeed evolve and (ii) this leads to an increase in the amount of cooperation in a population (Figure 4). In a two-player game, if memory has no cost, memory tends to increase over time, which in turn drives an increase in the frequency of cooperators and a decline in defectors. This is accompanied by a large overall increase in the population mean fitness. By contrast, when the game size is large,  $n = N$ , there is little evolutionary change in memory capacity and defection continues to be more frequent than cooperation even as strategies and memory co-evolve. When memory comes at a cost (Figure S3), an intermediate level of memory evolves for small  $n$ , and there is a correspondingly weaker increase in the degree of cooperation.

How are we to understand why memory evolves at all in these co-evolutionary simulations? The change in memory capacity is puzzling, at first glance, because a longer memory conveys no direct advantage against a resident robust strategy – since robustness implies uninvadability by any opponent, regardless of the opponent's memory capacity. The key to understanding this co-evolutionary pattern is to note that longer memories are, on average, better at *invading* non-robust strategies, due to their greater capacity for contingent punishment (Figure S3). Thus, when games are sufficiently small, the neutral drift that leads to turnover between cooperation and defection [3, 26] also provides opportunity for longer-memory strategies to invade and fix.

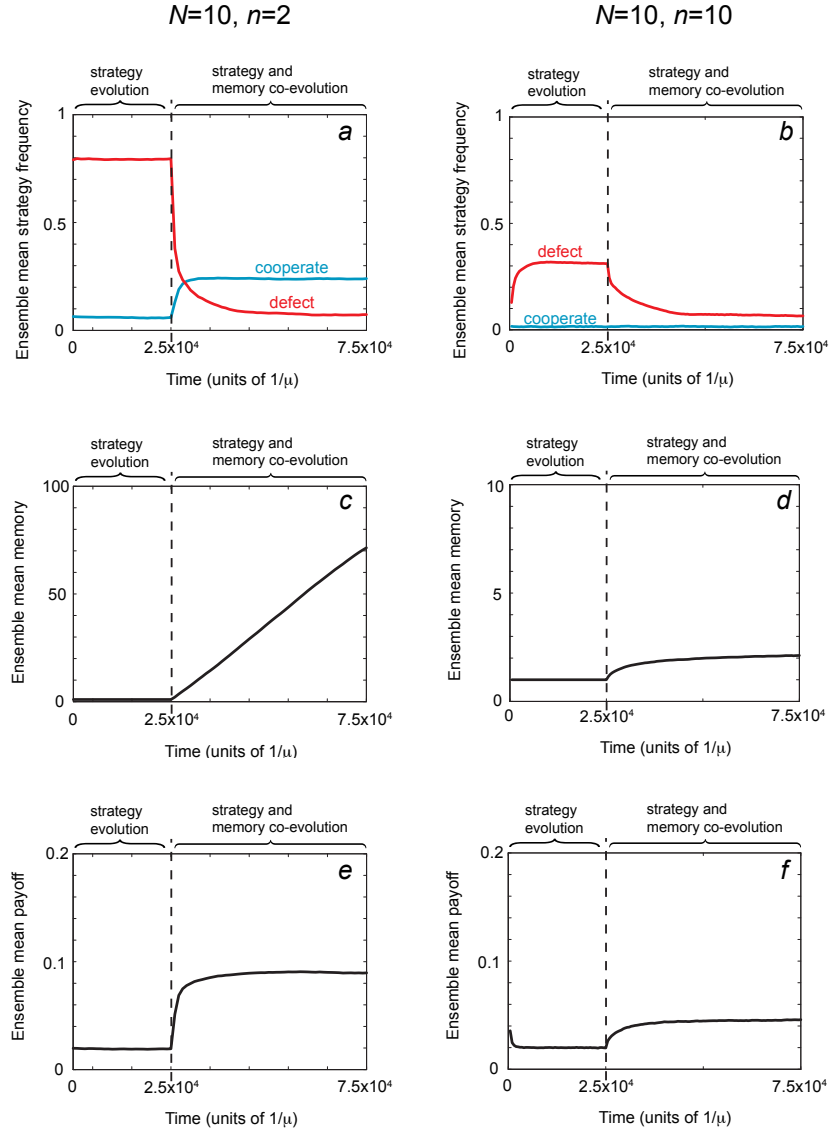


Figure 4: Co-evolution of strategies and memory capacity. We simulated populations playing the iterated  $n$ -player public-goods game, proposing mutant strategies until reaching equilibrium, and then also proposing mutations to a player's memory capacity  $m$ , each at rate  $\mu/10$ . In these simulations all players initially have memory  $m = 1$ , with payoff parameters  $C = 1$  and  $B = 1.2$ . Mutations to strategies were drawn uniformly from the full space of memory- $m$  strategies. Mutations perturbing the memory  $m$  caused it to increase or decrease by 1, with a lower bound of  $m = 1$ . Evolution was modeled according to a copying process under weak mutation [3] in a population of size  $N = 10$  individuals. (a) When the game size is small,  $n = 2$ , defecting strategies are initially dominant in the population, but they are quickly replaced by cooperators as memory capacity evolves to higher values. (b) When game size is large,  $n = N = 10$ , defecting strategies initially dominate the population and they remain dominant as memory evolves. In both (a) and (b) the overall frequency of cooperators and defectors decline as the dimension of strategy space increases, in line with the decline in the overall volume of robust strategies (Figure S4). (c) When the game size is small memory evolves rapidly to larger values, reflecting the greater success of longer-memory strategies at invading (Figure S3), and driving the increase in cooperative as compared to defecting strategies. (d) When the game size is large memory does not evolve to large values, reaching only  $m = 2$  across 50,000 generations, and reflecting the decline in long-memory strategies' success as invaders in larger games. (e) As cooperation increases so does the average payoff of the population, by a factor of 5-10 fold. (f) The lack of increase in cooperation results in a much more modest (although still appreciable) increase in average payoff for the population as defectors become less frequent.

## 2 Discussion

We have constructed a coordinate system that enables us to completely characterize the evolutionary robustness of arbitrary strategies in iterated multi-player public-goods games. This allows us to quantify the contrasting impacts of the number of players who engage in a game, and the memory capacity of those players, on the evolution of cooperative behavior and collective action. In particular we have shown that while increasing the number of players in a game makes both cooperation and longer memories harder to evolve, in small games, memory capacity tends to increase over time and drives the evolution of cooperative behavior.

To understand the evolution of social behavior it is not sufficient to simply determine whether particular types of strategies exist or not. Indeed, for repeated games, strategies that enforce any given social norm are guaranteed to exist by the famous Folk Theorems [35]. The more incisive question, from an evolutionary viewpoint, is how often strategies of different types arise via random mutation, how often they reach fixation, and how long they remain fixed in the face of mutant invaders and other evolutionary forces such as neutral genetic drift. To address these questions we have analyzed the evolutionary robustness of strategies that result in sustained cooperation. We have shown that a strategy is more likely to be evolutionary robust if it can successfully punish defectors. We have shown that players with longer memories have access to a greater volume of such evolutionary robust strategies, and that, as a result, over the course of evolution populations that evolve longer memories are more likely to evolve cooperative behaviors. Memory of the type we have considered does not result in better strategies per se, but in a greater quantity of robust cooperative strategies.

In contrast to memory capacity, larger games favor defecting strategies over cooperating strategies, because larger games reduce the marginal cost to a player of switching from cooperation to defection, and make it harder for even long-memory players to effectively punish defectors. Thus we find in evolutionary simulations that only in small games do both long-memory strategies and cooperation tend to evolve and dominate. It is important to emphasize that these effects are driven by changes in the volume of robust cooperative strategies.

A complex balance between behavior, memory, game size and environment can lead to wide variation in evolutionary outcomes in the presence of social interactions. Understanding this balance is vital if we are to understand and interpret the role of cooperative behavior in evolution. Despite the complexity of the problem, and the very general  $n$ -player memory- $m$  setting we have analyzed, we have arrived at a few simple qualitative predictions, which may admit to testing not only in the social interactions of natural populations [12] but also through experiments with human players [36, 37]. Of course, the type of memory discussed here is only a small part of the story. We have ignored the possibility of other kinds of memory, which allow players to “tag” one another [38, 39] after the completion of a game. We have ignored the role of spatial structure, of demographic structure, and of dispersal [5]. We have failed to specify the underlying mechanisms by which public-goods and players’ decisions are produced and executed. Accounting for all of these additional factors is an important challenge as researchers seek to elucidate the emergence of collective action in evolving populations and beyond.

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# Small games and long memories promote cooperation: Supporting information

Alexander J. Stewart<sup>\*1,2</sup>, Joshua B. Plotkin<sup>1</sup>

<sup>1</sup> Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

<sup>2</sup> Current address: Department of Genetics, Environment and Evolution, University College London, London, UK

\* E-mail: alstew@sas.upenn.edu

## 3 Overview of Supporting Information

In this supplement we detail our analysis of iterated  $n$ -player games in which players have two choices in each round and can remember the outcomes of the previous  $m$  rounds. We identify the strategies that are able to resist selective invasion by any other strategy in an evolving population of players. Such strategies are called “evolutionary robust”, as defined formally below. An iterated  $n$ -player game consists of an infinite series of “rounds” in each of which each player chooses to either “cooperate” ( $c$ ) or “defect” ( $d$ ). A memory- $m$  strategy stipulates that the probability of cooperation in the current round depends on the outcomes of the preceding  $m$  rounds. The full space of memory- $m$  strategies in such an  $n$ -player game thus has dimension  $2^{n \times m}$ . To identify strategies that are evolutionary robust across such a large space we first introduce a convenient coordinate transform for the space of memory- $m$  strategies, which generalizes that introduced to study memory-1 strategies in iterated 2-player games [1–3]. This coordinate transformation enables us to identify sets of memory- $m$  strategies that are robust to invasion by any other strategy in an evolving population. We apply this method to analyse evolutionary robustness in various  $n$ -player iterated public goods game.

### 3.1 Iterated $n$ -player games

We consider an iterated game with an infinite number of successive rounds between a player,  $X_0$  and her opponents  $X_1, X_2, \dots, X_{n-1}$ . We study games for which, in each round, each player has two choices, denoted cooperate ( $c$ ) and defect ( $d$ ). The payoffs in a given round to the focal player  $X_0$  is given by  $R_{c,l-1}$ , if she cooperates along with  $l-1$  of her opponents, and it is given by  $R_{d,l}$  if she defects while  $l$  of her opponents cooperate.

We will focus on public goods-type games, for which by definition in each round

- $R_{d,l} > R_{c,l-1}$  so that, given  $l$  players cooperating in total, those who defected receive a higher payoff than those who cooperated
- $R_{c,l} \geq R_{c,l-1}$  and  $R_{d,l} \geq R_{d,l-1}$  so that, typically, the more of her opponents cooperate, the higher the payoff a cooperative focal player receives.

We will focus in particular on the most typical type of public goods game, for which  $R_{c,l-1} = B \frac{l}{n} - C$  and  $R_{d,l} = B \frac{l}{n}$ , where  $B > C$ .

### 3.2 Memory- $m$ strategies

A memory- $m$  strategy takes account of the outcomes of the preceding  $m$  rounds of play among all players. As such in any given round there are  $n \times m$  plays taken into account, and the strategy space therefore has dimension  $2^{n \times m}$  – that is, a player’s strategy consists of  $2^{n \times m}$  probabilities for cooperation. First we develop notation to describe the probability that a focal player will cooperate in a focal round, given the plays made by all  $n$  players over the preceding  $m$  rounds. We denote the sequence of plays of the  $i$ th player over the preceding  $m$  rounds  $\sigma_i$ , which has elements  $\sigma_k^i$ , denoting the play of player  $i$ ,  $k$  steps in the past, where  $i = 0 \dots n - 1$  and  $k = 1 \dots m$ . Thus  $\sigma_k^i = c$  if player  $i$  cooperated and  $\sigma_k^i = d$  if she defected  $k$  steps in the past. We then write the probability for cooperation for a particular history of play in its most general form as  $p_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}} \in [0, 1]$ .

In order to determine the robustness of such strategies, it will be convenient to introduce the operator  $\theta$  which returns

$$\theta(\sigma_k^i) = \begin{cases} 1 & \text{if } \sigma_k^i = c \\ 0 & \text{if } \sigma_k^i = d \end{cases}$$

where for simplicity we will often write  $\theta_k^i$  in place of  $\theta(\sigma_k^i)$  for the play of the  $i$ th player  $k$  steps back in time. The number of times player  $i$  cooperated within memory is thus  $\sum_{k=1}^m \theta_k^i$  and the number of players who cooperated in the immediately preceding round is  $\sum_{i=0}^{n-1} \theta_1^i$ .

### 3.3 Equilibrium payoffs in Iterated Games

The longterm scores received by  $n$  memory- $m$  players in an infinitely iterated game are calculated from the equilibrium rates of the different plays. This can be determined from the stationary distribution a Markov chain on  $2^{n \times m}$  states, which correspond to the history of plays across the preceding  $m$  rounds. In order to do this we write the equilibrium rate of a particular history of plays as  $v_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}$ .

The essential trick we use to analyze equilibrium payoffs in multi-player games among players with long-memory strategies is to reduce the problem to an equivalent problem involving more players each using only memory-1 strategies. The advantage of the memory-1 setting is that it will allow us to express equilibrium payoffs in the framework of determinants developed by Press & Dyson and others ???. In particular, given a game among  $n$  players who memory- $m$  strategies we construct an equivalent  $n \times m$ -player game in which players use only memory-1 strategies. Of these  $n \times m$  players,  $n$  are “real” players, and they each use a memory-1 strategy that corresponds precisely to a memory- $m$  strategy in the original long-memory game, as described above. In order to allow the “real” memory-1 players to effectively react to the entire history of plays across  $m$  prior rounds we construct  $m - 1$  “shadow” players for each real player, who encode the information of earlier rounds. At each round, the shadow player with index  $k > 1$  deterministically executes the play of its associated real player,  $k$  rounds in the past.

Given an  $n$ -player game among memory- $m$  strategies, we encode the equivalent  $n \times m$ -player game among memory-1 strategies by writing  $\mathbf{p}^{i,k}$  as the vector of all  $2^{n \times m}$  probabilities for cooperation for the  $i$ th player,  $k$  steps in the past. If we order the players such that they are indexed from  $j = 1 \dots n \times m$  then the index of player  $i, k$  is given by  $j = i \times m + k$ . In this labelling system,  $\mathbf{p}^{i,1}$  is the strategy of the  $i$ th real player, and  $\mathbf{v}$  is the corresponding stationary vector of equilibrium rates of play. Finally we must encode the “strategy vector” of the shadow players, which encode how a player updates her memory each round. This is simple to do. We write  $\mathbf{p}^{i,k}$  as the “strategy” vector which updates the memory of player  $i$ ,  $k$  steps in the past (see Figure. S1 for illustration). This vector has entry 1 if  $\theta_{k-1}^i = 1$  and 0 if  $\theta_{k-1}^i = 0$ . Thus the real strategy of player  $i$  consists of probabilities  $\mathbf{p}^{i,1} \in [0, 1]^{n \times m}$ , whereas a shadow strategy, for which  $k > 1$ , consists of deterministic quantities  $\mathbf{p}^{i,k} \in \{0, 1\}^{n \times m}$ .

The equilibrium score of player  $X_0$  against players  $X_1, X_2, \dots, X_{n-1}$  is calculated according to a particular



form of determinant  $D$  defined below and written as:

$$S_1^0 = \frac{\mathbf{v} \cdot \mathbf{R}_1^0}{\mathbf{v} \cdot \mathbf{I}} = \frac{D(\mathbf{p}^{0,1}, \mathbf{p}^{0,2} \dots \mathbf{p}^{0,m}, \mathbf{p}^{1,1}, \mathbf{p}^{1,2} \dots \mathbf{p}^{1,m} \dots \mathbf{p}^{n-1,1}, \mathbf{p}^{n-1,2} \dots \mathbf{p}^{n-1,m}, \mathbf{R}^{0,1})}{D(\mathbf{p}^{0,1}, \mathbf{p}^{0,2} \dots \mathbf{p}^{0,m}, \mathbf{p}^{1,1}, \mathbf{p}^{1,2} \dots \mathbf{p}^{1,m} \dots \mathbf{p}^{n-1,1}, \mathbf{p}^{n-1,2} \dots \mathbf{p}^{n-1,m}, \mathbf{I})} \quad (4)$$

Note that in this expression have used the notation of the associated game with  $n \times m$ , memory-1 players,  $n$  of which correspond to the players in the original  $n$ -player, memory- $m$  game. In this equation  $\mathbf{I}$  denotes the identity vector of size  $2^{n \times m}$ , for which all elements are 1, and  $\mathbf{R}^{0,1}$  denotes the payoff vector of player  $X_0$ . The payoff to player 0 in a given round depends only on her own play and the plays of the  $n$  other players in that round. In general, the payoffs received by player  $i$ , in the round that occurred  $k$  steps previously is determined from the payoff vector  $\mathbf{R}^{i,k}$ , which has  $2^{n \times m}$  elements  $R_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}^{i,k}$  can be written as

$$R_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}^{i,k} = \begin{cases} R_{c, \sum_{j=0}^{n-1} \theta_k^j} & \text{if } \theta_k^i = 1 \\ R_{d, \sum_{j=0}^{n-1} \theta_k^j} & \text{if } \theta_k^i = 0 \end{cases} \quad (5)$$

Where for the standard public goods game we can write  $R_{c, \sum_{j=0}^{n-1} \theta_k^j} = \frac{b}{n} \sum_{j=0}^{n-1} \theta_k^j - c\theta_k^i$  and  $R_{d, \sum_{j=0}^{n-1} \theta_k^j} = \frac{b}{n} \sum_{j=0}^{n-1} \theta_k^j$ .

In general, the determinant  $D(\mathbf{p}^{0,1}, \mathbf{p}^{0,2} \dots \mathbf{p}^{0,m}, \mathbf{p}^{1,1}, \mathbf{p}^{1,2} \dots \mathbf{p}^{1,m} \dots \mathbf{p}^{n-1,1}, \mathbf{p}^{n-1,2} \dots \mathbf{p}^{n-1,m}, \mathbf{f})$  arises from a generalization of the results of Press & Dyson, [1] for two-player games, and of [4, 5] for multi-player games, and gives the dot product between the stationary vector  $\mathbf{v}$  and an arbitrary vector  $\mathbf{f}$  which has elements  $f_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}$ . In the example of a three player game with memory-1 strategies between players  $X_0$ ,  $X_1$  and  $X_2$  with strategies  $\mathbf{p}$ ,  $\mathbf{q}$  and  $\mathbf{r}$ , the determinant is given by

$$\det \begin{bmatrix} -1 + p_{c,c,c}q_{c,c,c}r_{c,c,c} & -1 + p_{c,c,c}q_{c,c,c} & -1 + p_{c,c,c}r_{c,c,c} & -1 + p_{c,c,c} & -1 + q_{c,c,c}r_{c,c,c} & -1 + q_{c,c,c} & -1 + r_{c,c,c} & f_{c,c,c} \\ p_{c,c,d}q_{c,c,d}r_{d,c,c} & -1 + p_{c,c,d}q_{c,c,d} & p_{c,c,d}r_{d,c,c} & -1 + p_{c,c,d} & q_{c,c,d}r_{d,c,c} & -1 + q_{c,c,d} & r_{d,c,c} & f_{c,c,d} \\ p_{c,d,c}q_{d,c,c}r_{c,d,c} & p_{c,d,c}q_{d,c,c} & -1 + p_{c,d,c}r_{c,d,c} & -1 + p_{c,d,c} & q_{d,c,c}r_{c,d,c} & q_{d,c,c} & -1 + r_{c,d,c} & f_{c,d,c} \\ p_{c,d,d}q_{d,c,d}r_{d,d,c} & p_{c,d,d}q_{d,c,d} & p_{c,d,d}r_{d,d,c} & -1 + p_{c,d,d} & q_{d,c,d}r_{d,d,c} & q_{d,c,d} & r_{d,d,c} & f_{c,d,d} \\ p_{d,c,c}q_{c,d,c}r_{c,c,d} & p_{d,c,c}q_{c,d,c} & p_{d,c,c}r_{c,c,d} & p_{d,c,c} & -1 + q_{c,d,c}r_{c,c,d} & -1 + q_{c,d,c} & -1 + r_{c,c,d} & f_{d,c,c} \\ p_{d,c,d}q_{c,d,d}r_{d,c,d} & p_{d,c,d}q_{c,d,d} & p_{d,c,d}r_{d,c,d} & p_{d,c,d} & q_{c,d,d}r_{d,c,d} & -1 + q_{c,d,d} & r_{d,c,d} & f_{d,c,d} \\ p_{d,d,c}q_{d,c,d}r_{c,d,d} & p_{d,d,c}q_{d,c,d} & p_{d,d,c}r_{c,d,d} & p_{d,d,c} & q_{d,d,c}r_{c,d,d} & q_{d,d,c} & -1 + r_{c,d,d} & f_{d,d,c} \\ p_{d,d,d}q_{d,d,d}r_{d,d,d} & p_{d,d,d}q_{d,d,d} & p_{d,d,d}r_{d,d,d} & p_{d,d,d} & q_{d,d,d}r_{d,d,d} & q_{d,d,d} & r_{d,d,d} & f_{d,d,d} \end{bmatrix} = D(\mathbf{p}_x, \mathbf{q}_y, \mathbf{r}_z, \mathbf{f}) = \quad (6)$$

Eq. 1 can be used to calculate the scores received by  $n$  memory-1 players in a given game. However, there are certain cases in which the Markov chain describing the iterated game has multiple absorbing states, and the denominator of Eq.1 goes to zero. The scores in these cases can be calculated by assuming that players execute their strategy with some small “error rate”  $\epsilon$  [6], so that the probability of cooperation is at most  $1 - \epsilon$  and at least  $\epsilon$ . Assuming this, and taking the limit  $\epsilon \rightarrow 0$  then gives the player’s scores in the cases where multiple absorbing states exist.

## 4 Evolution in a population of players

We study the evolution of memory- $m$  strategies in a population of  $N$  individuals playing an iterated  $n$ -player game, with  $N \geq n$ . In each generation, all subsets of  $n$  players in the population engage in the iterated game, and each player in the population receives a total score across all the  $\binom{N-1}{n-1}$  games in which she participates. We assume that the population is well-mixed, so that the makeup of different strategies these games depends upon the frequencies of strategies in the population. We focus on evolution under weak-mutation, in which a strategy  $X$  is resident in the population; a single mutant strategy  $Y$

arises through mutation; and  $Y$  is subsequently either lost or goes to fixation in the population, before another mutant arises. We always use  $X$  to denote the resident, and  $Y$  the mutant, strategy. Under this weak-mutation assumption there are at most two strategy types present in the population at any time.

We use the notation  $S_a^X$  to denote the payoff to strategy  $X$  in a single iterated game involving  $a$  players of type  $Y$  and  $n - a$  players of type  $X$ . We use the notation  $S_a^Y$  to denote the payoff to strategy  $Y$  in a single iterated game involving  $a$  players of type  $Y$  and  $n - a$  players of type  $X$ . When the population as a whole contains  $b$  players of type  $Y$  and  $N - b$  players of type  $X$ , then, the total score to a player of type  $X$ , denoted  $T^X(b)$ , is given by

$$T^X(b) = \frac{(N - n)!(n - 1)!}{(N - 1)!} \sum_{a=0}^{\min[b, n-1]} \frac{(N - 1 - b)!}{(N - b - (n - a))!(n - 1 - a)!} \frac{b!}{a!(b - a)!} S_a^X$$

where the sum over  $a$  denotes the different number of opponents of type  $Y$  that  $X$  may face in the  $n$ -player games she plays in a single generation. The total score to a mutant  $Y$  in such a population, denoted  $T^Y(b)$ , can be calculated in the same way.

We model evolution according to the copying process [7], in which pairs of players are drawn at random from the population, and the first player switches her strategy to that of the second player with a probability that depends on the difference between their total scores. Thus a player using a strategy  $X$  switches to  $Y$  with probability

$$f_{X \rightarrow Y} = \frac{1}{1 + \exp[s(T^X(a) - T^Y(a))]}$$

where  $s$  is a parameter denoting the strength of selection.

The “strong-selection” regime of this process occurs when  $Ns \gg 1$ . Under this regime selection is sufficiently strong that an invading mutant is extremely unlikely to reach high frequency in the population, unless it has a selective advantage (or is neutral) against the resident strategy in the population. Thus under strong selection, resident strategies that can resist invasion by all other mutants are evolutionary robust. Alternatively, the “weak-selection” limit arises when  $Ns \ll 1$  in which case even deleterious strategies may reach high frequency through genetic drift. We focus on the regime of strong selection in our analysis below.

## 4.1 Evolutionary robustness

The concept of evolutionary robustness [8] is similar to the notion of evolutionary stability [9, 10], but more useful for studying evolution in large strategy spaces, in which an ESS strategy typically does not exist [3, 8]. In general, a strategy is defined to be evolutionary robust if, when resident in a population, there is no mutant that is favored to spread by natural selection when rare [8].

More precisely, under strong selection a resident strategy  $X$  is evolutionary robust iff  $T^Y(1) \leq T^X(1)$  for all strategies  $Y$ . This condition for evolutionary robustness under strong selection is identical to that of a Nash equilibrium in the limit  $N \rightarrow \infty$ .

## 5 Coordinate Transform

In two-player games, the work of Press & Dyson [1] and Akin [2] allows us to identify a coordinate transform for the full space of memory-1 strategies. This coordinate transformation permits a simple closed-form expression relating the scores of two players in a game, which has enabled us to identify all evolutionary robust memory-1 strategies, under both strong and weak selection [3, 8]. Here we extend this line of analysis to multi-player games with memory- $m$  strategies. We begin by identifying an analogous coordinate transform for the  $2^{n \times m}$ -dimensional space of memory- $m$  strategies in an  $n$ -player game.

To define the desired co-ordinate transform we must identify  $2^{n \times m}$  vectors that form a basis in  $\mathbb{R}^{n \times m}$  and that allow us to write down a simple, closed-form relationship between the players' scores in a given game.

These vectors consist firstly of the  $n \times m + 1$  vectors  $\mathbf{R}_k^i$  for each player's payoff in the  $k$ th preceding round, along with the identity vector  $\mathbf{I}$ , with entry 1 in all positions. The second set of vectors in the coordinate transform consists of the  $n \times m - 1$  vectors denoted  $\mathbf{L}^l$ , where  $\mathbf{L}^l$  has entry 1 when  $l$  players cooperated in the previous  $m$  rounds and entry 0 otherwise, regardless of the focal player's play in the previous round. Note that this excludes the case where all players cooperated and the case where no players cooperated, which are accounted for by the identity vector.

The final  $2^{n \times m} - 2n \times m$  vectors required for the coordinate transform account for the degeneracy that arises due to the number of ways in which  $l$  players can cooperate in the preceding  $m$  rounds. Given  $l$ , if the focal player cooperates  $l_p$  times over  $m$  rounds, and her opponents therefore cooperate  $l_o = l - l_p$  times, she will receive the same total payoff over those  $m$  rounds in a standard public goods game, regardless of which players cooperated or when. In the most general case a player may nonetheless distinguish between the play of each player (including herself) in each of the preceding  $m$  rounds.

We already have  $2n \times m$  vectors, as described above. The simplest way to account for the remaining dimensions (required for players to distinguish between all possible outcomes) is simply to add

$$2 \sum_{l=1}^{n \times m - 1} \left( \frac{(n \times m - 1)!}{k!(n \times m - l - 1)!} - 1 \right) = 2^{n \times m} - 2n \times m$$

vectors, denoted  $\mathbf{G}_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}^{l_o, l_p}$ , which have entry 1 for a single set of plays  $(\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1})$ , for which  $\sum_{i=1}^{n-1} \sum_{k=1}^m \theta_k^i = l_o$  is the total number of times all players have cooperated in the last  $m$  rounds and  $\sum_{k=1}^m \theta_k^0 = l_p$  is the number of times the focal player has cooperated in the last  $m$  rounds. Note that we have written these vectors in terms of  $l_p$  and  $l_o$  in order to aid later analysis.

We adopt the convention that we do not add a vector  $\mathbf{G}_{\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1}}^{l_o, l_p}$  for the set of opponent plays which is ordered *cccc. . . dddd* across the ordered history of all players, and the set focal player plays ordered either *cccc. . . dddd* or *dccc. . . dddd*. That is, the play for which the first  $l_o$  terms of the sum  $\sum_{i=1}^{n-1} \sum_{k=1}^m \theta_k^i$  are 1, and either  $\theta_0^1 = 1$  and  $\sum_{k=1}^{l_p} \theta_k^i = l_p$  or else  $\theta_0^1 = 0$  and  $\sum_{k=1}^{l_p+1} \theta_k^i = l_p$ .

In summary, the  $2^{n \times m}$  vectors for the coordinate transform consist of

- $n \times m$  vectors  $\mathbf{R}$  for the player's payoffs, and the vector  $\mathbf{I}$ .
- $n \times m - 1$  vectors  $\mathbf{L}^l$  with entry 1 when  $l$  players cooperated in the previous round.
- $2^{n \times m} - 2n \times m$  vectors  $\mathbf{G}$  with a single entry 1, to account for the degeneracy which arises when different combinations of opponents cooperate.

Although this is a somewhat complex transformation, we shall see the utility of working this way in what follows.

For clarity's sake we can write down this coordinate system explicitly, first for the case of  $n = 3$  players with memory-1. The new coordinate system is  $\left\{ \mathbf{R}_1^0, \mathbf{R}_1^1, \mathbf{R}_1^2, \mathbf{I}, \mathbf{L}^1, \mathbf{L}^2, \mathbf{G}_{c,d,c}^{1,1}, \mathbf{G}_{d,d,c}^{1,0} \right\}$  and we have

$$\det \begin{bmatrix} R_{c,2} & R_{c,2} & R_{c,2} & 1 & 0 & 0 & 0 & 0 \\ R_{c,1} & R_{c,1} & R_{d,2} & 1 & 1 & 0 & 0 & 0 \\ R_{c,1} & R_{d,2} & R_{c,1} & 1 & 1 & 0 & 1 & 0 \\ R_{c,0} & R_{d,1} & R_{d,1} & 1 & 0 & 1 & 0 & 0 \\ R_{d,2} & R_{c,1} & R_{c,1} & 1 & 1 & 0 & 0 & 0 \\ R_{d,1} & R_{c,0} & R_{d,1} & 1 & 0 & 1 & 0 & 0 \\ R_{d,1} & R_{d,1} & R_{c,0} & 1 & 0 & 1 & 0 & 1 \\ R_{d,0} & R_{d,0} & R_{d,0} & 1 & 0 & 0 & 0 & 0 \end{bmatrix} = -3(R_{c,2} - R_{d,0})(R_{d,1} - R_{c,0})(R_{d,2} - R_{c,1}) \quad (7)$$

which is therefore a basis  $\mathbb{R}^8$ . Similarly, for the case of  $n = 2$  players with with memory- $m$  the new coordinate system is  $\{\mathbf{R}_1^0, \mathbf{R}_1^1, \mathbf{R}_2^0, \mathbf{R}_2^1, \mathbf{I}, \mathbf{L}^1, \mathbf{L}^2, \mathbf{L}^3, \mathbf{G}_{dd,cd}^{1,0}, \mathbf{G}_{dd,dc}^{1,0}, \mathbf{G}_{dd,cc}^{2,0}, \mathbf{G}_{dc,dc}^{1,1}, \mathbf{G}_{cd,cd}^{1,1}, \mathbf{G}_{cd,dc}^{1,1}, \mathbf{G}_{cc,dc}^{1,2}, \mathbf{G}_{cd,cc}^{2,1}\}$  and we have

$$\det \begin{bmatrix} R_{c,2} & R_{c,2} & R_{c,2} & R_{c,2} & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{c,2} & R_{c,1} & R_{c,2} & R_{d,1} & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{c,2} & R_{d,1} & R_{c,2} & R_{c,1} & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ R_{c,2} & R_{d,0} & R_{c,2} & R_{d,0} & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ R_{c,1} & R_{c,2} & R_{d,1} & R_{c,2} & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ R_{c,1} & R_{c,1} & R_{d,1} & R_{d,1} & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{c,1} & R_{d,1} & R_{d,1} & R_{c,1} & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ R_{c,1} & R_{d,0} & R_{d,1} & R_{d,0} & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,1} & R_{c,2} & R_{c,1} & R_{c,2} & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,1} & R_{c,1} & R_{c,1} & R_{d,1} & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,1} & R_{d,1} & R_{c,1} & R_{c,1} & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ R_{d,1} & R_{d,0} & R_{c,1} & R_{d,0} & 1 & 1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,0} & R_{c,2} & R_{d,0} & R_{c,2} & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ R_{d,0} & R_{c,1} & R_{d,0} & R_{d,1} & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,0} & R_{d,1} & R_{d,0} & R_{c,1} & 1 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ R_{d,0} & R_{d,0} & R_{d,0} & R_{d,0} & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} = -4(R_{c,2} - R_{d,0})^2(R_{d,1} - R_{c,1})^2 \quad (8)$$

which is therefore a basis  $\mathbb{R}^{16}$ .

Using the results of Press & Dyson, generalised to multi-player games [1,4,5], the strategy of the focal player in this coordinate new system, which for convenience we assign index  $i = 0$ , is given by a vector of the form:

$$\mathbf{p}^{0,1} - \boldsymbol{\theta}_1^0 = \sum_{i=0}^{n-1} \sum_{k=1}^m \alpha_k^i \mathbf{R}_k^i + \alpha_n \mathbf{1} + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left[ \lambda_{l_o+l_p} \mathbf{L}^{l_o+l_p} + \sum_{\boldsymbol{\sigma} \in \mathcal{H}_{o,p}} \gamma_{\boldsymbol{\sigma}}^{l_o, l_p} \mathbf{G}_{\boldsymbol{\sigma}}^{l_o, l_p} \right]. \quad (9)$$

where we define  $\mathcal{H}_{o,p} = \{(\sigma_0, \dots, \sigma_n) | \sum_{k=1}^m \theta_k^0 = l_p, \sum_{i=1}^{n-1} \sum_{k=1}^{m-1} \theta_k^i = l_o\}$  is the set of combinations of plays by  $n$  players across the last  $m$  rounds such that player 0 (the focal player) cooperated  $l_p$  times and her oppoennts cooperated a total  $l_o$  times. Note that we set  $\lambda = \gamma = 0$  when  $l_o = l_p = 0$  and  $l_o + l_p = n \times m$ . The vector  $\boldsymbol{\theta}_1^0$  has the corresponding elements  $\theta_1^0$  for the play of the focal player in the preceding round (i.e 1 if she cooperated and 0 if she defected), and we have written  $\boldsymbol{\sigma} = (\sigma_0, \dots, \sigma_n)$ .

From Eq.1 the scores of the players are then related by the expression

$$\sum_{i=0}^{n-1} \sum_{k=1}^m \alpha_k^i S^i + \alpha_n \mathbf{1} + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left[ \lambda_{l_o+l_p} v_{\sigma}^{l_o, l_p} + \sum_{\sigma \in \mathcal{H}_{o,p}} \gamma_{\sigma}^{l_o, l_p} v_{\sigma}^{l_o, l_p} \right] = 0. \quad (10)$$

where  $S^i$  denotes the equilibrium score of player  $i$  in the current game,  $v_{\sigma}^{l_o+l_p}$  denotes the rate at which  $l_o + l_p$  players cooperate and  $v_{\sigma}^{l_o, l_p}$  is the rate at which the focal player cooperates  $l_p$  times, along with  $l_o$  of her opponents, with the sequence of plays following the ordering  $\sigma = (\sigma_0, \sigma_1, \sigma_2, \dots, \sigma_{n-1})$ . Note that the equilibrium score of player  $i$  is independent of  $k$  in Eq. 7.

We now additionally define the parameters  $\chi_k^0 = -\alpha_k^0$ ;  $\phi_{i \times m+k} = \alpha_k^i$ ; and  $\kappa (\sum_{k=1}^m (\chi_k^0 - \sum_{i=1}^n \phi_{i \times m+k})) = \alpha_n$ . In this new parameterization we can re-write the relationship among the players' scores as:

$$\sum_{k=1}^m \left( \sum_{i=1}^{n-1} \phi_{i \times m+k} (S^i - \kappa) - \chi_k^0 (S^0 - \kappa) \right) + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left[ \lambda_{l_o+l_p} v_{\sigma}^{l_o, l_p} + \sum_{\sigma \in \mathcal{H}_{o,p}} \gamma_{\sigma}^{l_o, l_p} v_{\sigma}^{l_o, l_p} \right] = 0 \quad (11)$$

Eq.8 gives the most general form for the relationship between player's scores in an  $n$ -player game with memory- $m$ . Henceforth we will restrict our analysis restricted to a focal strategy in which a memory- $m$  player does not distinguish between her opponents, and does not pay attention to the order of cooperation events. As such we consider a focal player who keeps track of two quantities: (i) the total number of times her opponents cooperated in the last  $m$  rounds and (ii) the total number of times she cooperated in the last  $m$  rounds.

## 5.1 Strategies that track cooperation frequency

If a focal player tracks only the number of times she cooperated in the last  $m$  rounds, and the total number of times her opponent cooperated in the last  $m$  rounds, then her memory- $m$  strategy consists of  $((n-1)m+1) \times (m+1)$ , since her  $(n-1)$  opponents can cooperate anywhere between 0 and  $(n-1)m$  times in  $m$  rounds, and she can cooperate anywhere between 0 and  $m$  times, to give a strategy consisting of  $((n-1)m+1) \times (m+1)$  probabilities for cooperation. We will henceforth explicitly adopt a standard public goods payoff structure, with  $R_{c,l} = B_n^l - C$  and  $R_{d,l} = B_n^l$

Eq. 6 encodes a strategy with  $2^{n \times m}$  probabilities for cooperation, many of which are redundant in our reduced strategy space. Let the focal player cooperate  $l_p$  times and her opponents cooperate  $l_o$  times in  $m$  rounds.

Starting from Eq. 8 are now able to make two observations:

(i) If the focal player does not distinguish between opponents, or the order in which they cooperate, then her payoff, and the equilibrium rate of play  $v_{\sigma}^{l_o, l_p}$  are the same for all  $((n-1) \times m)! \times m!$  orderings of opponents and plays. Summing over all possible orderings of opponents and dividing by  $((n-1) \times m)! \times m!$  results in the equilibrium scores being related by

$$\phi \sum_{j=1}^{n-1} \frac{S^j}{n-1} - \sum_{k=1}^m \chi_k^0 (S^0 - \kappa) - \kappa \phi + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left[ \lambda_{l_o+l_p} + \gamma_{\sigma}^{l_o, l_p} \right] v_{\sigma}^{l_o, l_p} = 0 \quad (12)$$

where we have set  $\phi = \sum_{i=1}^{n-1} \sum_{k=1}^m \phi_{i \times m+k}$  and  $\frac{l_p!(m-l_p)!}{m!} \frac{l_o!((n-1) \times m - l_o)!}{((n-1) \times m)!} \sum_{\sigma \in \mathcal{H}_{o,p}} \gamma_{\sigma}^{l_o, l_p} = \gamma_{\sigma}^{l_o, l_p}$ , and the  $\gamma$  terms result from noting that, when summing over all orderings of opponents and events, a given term  $\gamma_{\sigma}^{l_o, l_p}$  is multiplied by each rate of play  $v_{\sigma}^{l_o, l_p}$  a total

$$\frac{m!}{l_p!(m-l_p)!} \frac{((n-1) \times m)!}{l_o!((n-1) \times m - l_o)!}$$

(ii) If we then sum over all  $\frac{m!}{l_p!(m-l_p)!} \frac{((n-1) \times m)!}{l_o!((n-1) \times m - l_o)!}$  degenerate probabilities for a given  $l_o$  and  $l_p$  we then arrive at

$$-\frac{l_p}{m} + p^{l_o, l_p} = -\frac{l_o}{(n-1) \times m} C\phi + B \frac{l_o + l_p}{n \times m} \left( \phi - \sum_{k=1}^m \chi_k^0 \right) + \sum_{k=1}^m \chi_k^0 C \frac{l_p}{m} - \left( \phi - \sum_{k=1}^m \chi_k^0 \right) \kappa + \lambda_{l_o + l_p} + \gamma^{l_o, l_p}.$$

as the expression for the probability of cooperation given that the focal player cooperated  $l_p$  times and her opponents  $l_o$  times in the last  $m$  rounds, assuming she only tracks cooperation frequency.

## 5.2 Boundary conditions

If we recall our convention that the equation lacking a  $\gamma$  is that which is ordered with *cccc.....dddd* etc we then have the following boundary conditions

$$-1 + p^{l_o, m} = -C \sum_{i=1}^{l_o} \phi_i + B \frac{l_o + l_p}{n \times m} \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) + \sum_{k=1}^m \chi_k^0 C - \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) \kappa + \lambda_{l_o + m}$$

and

$$-1 + p^{0, l_p} = B \frac{l_p}{n \times m} \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) + \sum_{k=1}^{l_p} \chi_k^0 C - \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) \kappa + \lambda_{l_p}$$

Similarly the term with *dccc.....dddd* lacks a  $\gamma$  terms so that

$$p^{l_o, m-1} = -C \sum_{i=1}^{l_o} \phi_i + B \frac{l_o + l_p}{n \times m} \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) + \sum_{k=2}^m \chi_k^0 C - \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) \kappa + \lambda_{l_o + m-1}$$

and

$$p^{0, l_p} = B \frac{l_p}{n \times m} \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) \phi + \sum_{k=2}^{l_p+1} \chi_k^0 C - \left( \sum_{i=1}^{l_o} \phi_i - \sum_{k=1}^m \chi_k^0 \right) \kappa + \lambda_{l_p}$$

First, combining the two expressions for  $p^{0, l_p}$  gives

$$\phi C \chi_{l_p+1}^0 = 1 + \phi C \chi_1^0$$

and since this must hold for all  $l_p$  we have  $\chi_{l_p+1}^0 = \chi_m^0$  is constant, and

$$\phi = \frac{1}{C(\chi_m^0 - \chi_1^0)} \quad (13)$$

Substituting these into the general expression for  $p^{0, l_p}$  we find

$$\gamma^{0, l_p} = 0$$

Second, combining the expressions for  $p^{l_o, m}$  and  $p^{l_o, m-1}$  gives

$$\phi \gamma^{l_o, m} = \frac{m-1}{m} + \phi C \frac{m-1}{m} (\chi_1^0 - \chi_m^0) + \phi \gamma^{l_o, m-1}$$

Substituting for  $\phi$  we then find

$$\gamma^{l_o, m} = \gamma^{l_o, m-1}$$

Finally, since  $\gamma^{(n-1) \times m} = 0$  by definition this also implies

$$\gamma^{(n-1) \times m, m-1} = 0$$

We therefore have  $((n-1) \times m + 1)(m+1) - (n \times m + 2)$  parameters  $\gamma^{l_o, l_p}$ , plus  $n \times m - 1$  parameter  $\lambda_{l_o, l_p}$ , plus 3 parameters  $\chi$ ,  $\phi$  and  $\kappa$  to give a total  $((n-1) \times m + 1)(m+1)$  parameters as required. We can use these boundary conditions for  $\gamma$  to construct the inverse coordinate transform. We arrive at the three simultaneous equations which can be solved for  $\kappa$ ,  $\chi$  and  $\phi$ :

$$\begin{aligned} \sum_{i=1}^{(n-1) \times m-1} (p^{i, m} - p^{i, m-1}) - (p^{(n-1) \times m, m-1} - p^{0, m}) &= (n-1) - C(n-1)\chi - C\phi \\ p^{0, 0} &= \kappa(\phi - \chi) \\ p^{(n-1) \times m, m} &= 1 + \kappa(\phi - \chi) - (B - C)(\phi - \chi) \end{aligned}$$

with the remaining terms  $\Lambda^{l_o, l_p}$  being determined by these three parameters plus  $p^{l_o, l_p}$ . Finally, we set

$$\chi = \chi_1^0 + (m-1)\chi_m^0 \quad (14)$$

and

$$\Lambda^{l_o, l_p} = \lambda_{l_o + l_p} + \gamma^{l_o, l_p} \quad (15)$$

to define a coordinate system characterized by a vector of  $((n-1) \times m + 1)(m+1)$  numbers,  $(\kappa, \chi, \phi, \Lambda^{0,0}, \dots, \Lambda^{(n-1) \times m, m})$  where we have conditions  $\Lambda^{0,0} = \Lambda^{(n-1) \times m, m} = 0$  and a third linear condition as described above.

### 5.3 Strategies and payoffs in a public goods game

We can now write the relationship between the players' scores when players do not pay attention to the identity of their opponents as

$$\phi \sum_{i=1}^{n-1} \frac{S^i}{n-1} - \chi(S^0 - \kappa) - \phi\kappa + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \Lambda^{l_o, l_p} v^{l_o, l_p} = 0.$$

In the case when one player uses strategy  $Y$  and the rest use strategy  $X$  we then have the following relationship between scores:

$$\phi S^Y \frac{1}{n-1} + \phi S^X \frac{n-2}{n-1} - \chi(S^X - \kappa) - \phi\kappa + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \Lambda^{l_o, l_p} v^{l_o, l_p} = 0. \quad (16)$$

The strategy of a focal player in a public goods game can then be written as

$$p^{l_o, l_p} = \frac{l_p}{m} + \kappa(\phi - \chi) + \left( B \frac{l_o + l_p}{n \times m} - C \frac{l_p}{m} \right) \chi - \left( B \frac{l_o + l_p}{n \times m} - C \frac{l_o}{(n-1) \times m} \right) \phi - \Lambda^{l_o, l_p} \quad (17)$$

Since a viable strategy must have  $0 \leq p^{l_o, l_p} \leq 1$  we see by looking at  $p^{0,0}$  and  $p^{(n-1) \times m, m}$  that

$$0 \leq \kappa \leq B - C$$

and

$$\phi > \chi$$

with additional constraints on the other parameters. This in turn implies that a cooperator, for which  $p^{(n-1) \times m, m} = 1$  necessitates  $\kappa = B - C$  and a defector, for which  $p^{0,0} = 0$  necessitates  $\kappa = 0$ .

## 6 Equilibrium rates of play

We now derive some inequalities that, in combination with Eq. 11, will allow us to identify the strategies that are evolutionary robust in  $n$ -player games. In general, we can write the score of a focal player with resident strategy  $X$  as

$$S^X = \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left( B \frac{l_o + l_p}{n \times m} - C \frac{l_p}{m} \right) v^{l_o, l_p}$$

Similarly the score of an opponent with a strategy  $Y$ , is given by

$$S^Y = \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left( B \frac{l_o + l_p}{n \times m} - C \frac{l_p}{m} \right) w^{l_o, l_p}$$

where  $w^{l_o, l_p}$  are the equilibrium rates of play from  $Y$ 's perspective. When there is only a single  $Y$  mutant in a game, then from  $Y$ 's perspective, all opponents are identical and use strategy  $X$ . In this situation we can write

$$v^{l_o, l_p} = \sum_{l'_p = \max[0, l_o + l_p - (n-1) \times m]}^{\min[m, l_o]} w^{l_o + l_p - l'_p, l'_p} \frac{((n-1) \times m - l_o - l_p + l'_p)!}{(m - l_p)!((n-2) \times m - l_o + l'_p)!} \frac{(l_o + l_p - l'_p)!}{l_p!(l_o - l'_p)!} \frac{m!((n-2) \times m)!}{((n-1) \times m)!} \quad (18)$$

where we assume  $w^{l_o + l_p - l'_p, l'_p} = 0$  for the unphysical case  $l'_p > l_o$ . This allows us to write the score of  $X$  in terms of  $w^{l_o, l_p}$ . We will now use these results to explore two special cases of interest: (i) The effect of increasing the size of the game  $n$  with fixed memory, and (ii) the effect of increasing memory size  $m$  with fixed game size.



## 7 Bounds on players' scores

We can now use Eq. 14 to find upper and lower bounds on the difference and the sum of players' scores, in the case that the game contains a single player using a strategy  $Y$  and  $n - 1$  players using a strategy  $X$ .

$$S^X = \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left( B \frac{l_o + l_p}{n \times m} - C \frac{l_o}{(n-1) \times m} \right) w^{l_o, l_p}$$

We can now write the difference between the scores of  $X$  and  $Y$  scores as

$$S^X - S^Y = \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m C \frac{l_p(n-1) - l_o}{(n-1) \times m} w^{l_o, l_p}$$

which enables us to identify upper and lower bounds on the difference between two players' scores, namely

$$S^X - S^Y \geq - \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m C \frac{l_o}{(n-1) \times m} w^{l_o, l_p} \quad (19)$$

which becomes an equality when  $Y$  always defects at equilibrium and

$$S^X - S^Y \leq \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m C \frac{(n-1) \times m - l_o}{(n-1) \times m} w^{l_o, l_p} \quad (20)$$

which becomes an equality when  $Y$  never defects at equilibrium. We can similarly write, for the sum of the player's scores,

$$S^X + S^Y \frac{1}{n-1} = \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m (B - C) \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}.$$

This gives an upper bound on the sum

$$S^X + S^Y \frac{1}{n-1} \leq \frac{n}{n-1} (B - C) - \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m (B - C) \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p}. \quad (21)$$

which becomes an equality when  $w^{0,0} = 0$  at equilibrium (i.e it is never the case that all players defect). Finally we have a lower bound on the sum

$$S_1^X + S_1^Y \frac{1}{n-1} \geq \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m (B - C) \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}. \quad (22)$$

which becomes an equality when  $w^{(n-1) \times m, m} = 0$ , (i.e it is never the case that all players cooperate at equilibrium).

It is also convenient to rewrite Eq. 12 for the relationship between two player's scores in terms of  $w$  to give

$$S^Y \frac{1}{n-1} + S^X \frac{n-2}{n-1} - (\chi_1^0 + (m-1)\chi_m^0)(S^X - \kappa) - \kappa + \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \left( \sum_{k=\max[0, l_o+l_p-(n-1) \times m]}^{\min[m, l_o]} \Lambda^{l_o+l_p-k, k} \frac{((n-1) \times m - l_o)!}{(m-k)!((n-2) \times m - l_o + k)!} \frac{l_o!}{k!(l_o-k)!} \frac{m!((n-2) \times m)!}{((n-1) \times m)!} \right) w^{l_o, l_p} = 0. \quad (23)$$

We can now use Eqs. 16-20 to identify the strategies that are evolutionary robust, under strong selection, in multi-player games.

## 7.1 Robust strategies

We focus here on the prospects for cooperation in iterated games. In particular, we identify strategies which, when used by all players in a game, ensure that all players cooperate. This is achieved quite simply by setting  $p^{n-1,1} = 1$  so that if all players cooperated in the preceding round, all players assuredly cooperate in the following round. We call these strategies the cooperators and we calculate the robustness of these strategies by determining the proportion of cooperators that can resist invasion by all other strategies. We contrast this to the defectors: strategies which have  $p^{0,0} = 0$ , such that if all players defected in the preceding round, all players assuredly defect in the following round. The importance of these two strategy classes in two-player public goods games has been established already [3], making it natural to generalise their study to games with multiple players and long memory.

To determine whether a strategy is robust we use the condition given previously for an evolving population of  $N$  players in a multiplayer game. Given a resident strategy  $X$  in a population, selection acts against a new mutant  $Y$  provided  $T^X(1) > T^Y(1)$ , as described above. This can be written explicitly in terms of players' scores as

$$\frac{N-n}{N-1} S_0^X + \frac{n-1}{N-1} S_1^X > S_1^Y \quad (24)$$

where  $S_0^X$  is the score received by  $X$  with no mutants in the game,  $S_1^X$  is the score received by  $X$  with one mutant player  $Y$  in the game and  $S_1^Y$  is the score received by  $Y$  with no other mutants in the game.

## 7.2 Robust cooperating strategies under strong selection

We first identify the cooperating strategies that are robust under strong selection. As defined above, a cooperating strategy  $X$  is such that, if all players use the strategy, all players cooperate every turn at equilibrium. Such strategies must have  $\kappa = B - C$ .

A mutant strategy  $Y$  can selectively invade a cooperating strategy under strong selection iff

$$S_1^Y - S_1^X > \frac{N-n}{N-1} (B - C - S_1^X)$$

The longterm payoffs must additionally satisfy Eq. 17-21. We can therefore identify strategies  $X$  which cannot be selectively invaded by any mutant  $Y$ . For simplicity we write

$$\hat{\Lambda}^{l_o, l_p} = \sum_{k=\max[0, l_o+l_p-(n-1) \times m]}^{\min[m, l_o]} \Lambda^{l_o+l_p-k, k} \frac{((n-1) \times m - l_o)!}{(m-k)!((n-2) \times m - l_o + k)!} \frac{l_o!}{k!(l_o-k)!} \frac{m!((n-2) \times m)!}{((n-1) \times m)!}. \quad (25)$$

**Case I: Robustness when  $\chi \leq \frac{N(n-2)+1}{(N-1)(n-1)}\phi$**

Using Eq. 19 we can write the condition for invasion by a mutant strategy  $Y$  as

$$\left( \frac{N(n-2)+1}{(N-1)(n-1)}\phi - \chi \right) (S_1^X - (B-C)) < - \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \quad (26)$$

combining Eq. 15 with Eq. 19 then gives

$$\frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} < C \left( \frac{N(n-2)+1}{(N-1)(n-1)}\phi - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m C \frac{l_o}{(n-1) \times m} w^{l_o, l_p} \quad (27)$$

as a necessary condition for invasion.

**Case II: Robustness when  $\chi > \frac{N(n-2)+1}{(N-1)(n-1)}\phi$**

Combining Eq. 17 and Eq. 19 we can also write

$$\frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} < (B-C) \left( \frac{N(n-2)+1}{(N-1)(n-1)}\phi - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p} \quad (28)$$

as a necessary condition for robustness.

Thus, in summary, the set of robust cooperating strategies in an  $n$ -player game under strong selection with memory- $m$ , which we denote  $\mathcal{C}_s^{n,m}$ , is given by:

$$\begin{aligned} \mathcal{C}_s^{n,m} = & \left\{ (\chi, \phi, \kappa, \Lambda^{0,1}, \dots, \Lambda^{(n-1) \times m, m-1}) \middle| \kappa = B-C, \right. \\ & \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq C \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}, \\ & \left. \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq (B-C) \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p} \right\} \quad (29) \end{aligned}$$

### 7.3 Robust defecting strategies under strong selection

We now identify the defecting strategies that are robust under strong selection. As defined above, a defecting strategy  $X$  is one such that, if all players adopt the strategy, all players defect every turn at equilibrium. Such strategies must have  $\kappa = 0$ .

A mutant strategy  $Y$  can selectively invade a defecting strategy under strong selection iff

$$S_1^X - S_1^Y < \frac{N-n}{N-1} S_1^X$$

Using Eq. 19 this can be re-written as

$$S_1^X \left( \frac{N(n-2)+1}{(N-1)(n-1)} \phi - \chi \right) < -\frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \quad (30)$$

Following the same procedure as for the cooperators above, we find that the set of robust defecting strategies in an  $n$ -player game under strong selection with memory- $m$ , which we denote  $\mathcal{D}_s^{n,1}$ , is given by

$$\begin{aligned} \mathcal{D}_s^{n,m} = & \left\{ (\chi, \phi, \kappa, \Lambda^{0,1}, \dots, \Lambda^{(n-1) \times m, m-1}) \middle| \kappa = 0, \right. \\ & \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq -(B-C) \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{l_o + l_p}{(n-1) \times m} w^{l_o, l_p}, \\ & \left. \frac{N-n}{N-1} \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \hat{\Lambda}^{l_o, l_p} w^{l_o, l_p} \geq -C \left( \phi \frac{N(n-2)+1}{(N-1)(n-1)} - \chi \right) \sum_{l_o=0}^{(n-1) \times m} \sum_{l_p=0}^m \frac{n \times m - l_o - l_p}{(n-1) \times m} w^{l_o, l_p} \right\} \quad (31) \end{aligned}$$

Notice that in the special case  $n = N$ , in which all members of a population play the same public goods game together, the conditions for robustness are independent of  $\Lambda^{l_o, l_p}$ .

## 7.4 Calculating robust volumes

We have now derived necessary and sufficient conditions for cooperators and defectors to be robust in  $n$ -player public goods games. However, in contrast to the case of two-player games these conditions depend explicitly on the equilibrium play  $w^{l_o, l_p}$  of an invading mutant. We can nonetheless easily construct strategies that are assuredly robust, by using the fact that  $w^{l_o, l_p} \leq 1$  for all possible mutants. Similarly we can construct strategies that are assuredly invadable. However this leaves a large subset of strategies whose robustness depends on the actual values of  $w^{l_o, l_p}$ . Nonetheless we can still determine their robustness by using the fact that the bounds on players scores render the conditions Eqs. 26 and 27 most stringent when a mutant plays such that (1) he never cooperates at equilibrium (Eq. 16), (2) he plays so that  $w^{0,0} = 0$  at equilibrium, i.e so that all players do not defect simultaneously (Eq. 18), (3) he always cooperates at equilibrium (Eq. 17) or (4) he plays such that all players do not cooperate simultaneously (Eq. 19). This leaves us with four possible trigger strategies to test in order to determine the robustness of a cooperator or defector strategy (where the relevant trigger strategy depends on the values of  $\phi$  and  $\chi$  and whether the resident is a cooperator or a defector).

Figure 3 of the main text verifies the use of these four trigger strategies by comparing the analytically predicted volumes of robust strategies to those estimated by Monte Carlo against a large number of randomly chosen mutant invaders. This type of Monte Carlo verification is also shown in Figure S1 for the effect of population size  $N$  on the volume of robust strategies. As discussed in the main text, larger populations lead to larger volumes of robust cooperators and smaller volumes of robust defectors.

## 7.5 The impact of memory on robustness

As discussed in the main text, the impact of memory on robustness arises because it increases the capacity for contingent punishment, as expressed through the parameters  $\Lambda^{l_o, l_p}$ . The way in which this occurs is most clearly understood by looking at the expectation  $\langle \Lambda^{l_o, l_p} \rangle$  for a randomly drawn strategy. For a randomly drawn cooperating or defecting strategy the expectations  $\langle \chi \rangle$  and  $\langle \phi \rangle$  are related according to

$$\begin{aligned}(n-1) \langle \chi \rangle &= \frac{(n-1)}{C} - \langle \phi \rangle \\ 1/2 &= (B-C)(\langle \phi \rangle - \langle \chi \rangle)\end{aligned}$$

which gives

$$\begin{aligned}\langle \chi \rangle &= \frac{n-1}{Cn} - \frac{1}{2(B-C)n} \\ \langle \phi \rangle &= \frac{n-1}{Cn} + \frac{n-1}{2(B-C)n}\end{aligned}$$

The expectation  $\langle \Lambda^{l_o, l_p} \rangle$  for a randomly drawn cooperator is then

$$\langle \Lambda^{l_o, l_p} \rangle = \frac{1}{2} \frac{l_o + l_p}{n \times m}$$

which gives an average across all  $l_o, l_p$  of

$$\langle \Lambda \rangle = \frac{1}{4}$$

Similarly, the expectation  $\langle \Lambda^{l_o, l_p} \rangle$  for a randomly drawn defector is and the average  $\Lambda$  is

$$\langle \Lambda^{l_o, l_p} \rangle = -\frac{1}{2} \frac{n \times m - (l_o + l_p)}{n \times m}$$

which gives an average across all  $l_o, l_p$  of

$$\langle \Lambda \rangle = -\frac{1}{4}$$

If we now use Eq. 22 to determine the average  $\langle \hat{\Lambda}^{l_o, l_p} \rangle$  for a cooperators and defectors faced with a mutant who cooperated  $l_p$  times within their memory, we recover Fig S2. We see that a randomly drawn cooperator tends to be more succesful at punishing a given mutant, while a randomly drawn defector tends to become less successful, as memory increases.

## 7.6 Invasability and cost of memory

Our evolutionary simulations, Figure 4, show that in addition to increasing the overall robustness of cooperation, memory capacity  $m$  tends to increase in small games. To understand this we must look at the average fixation probability of mutations that increase memory by 1, versus those that decrease memory by 1. This is shown in Figure S2c. We see that mutations that increase memory capacity are more likely to fix than mutations that decrease memory capacity, regardless of the current resident

memory capacity. Thus longer memories will tend to evolve on average. If we introduce a cost for memory, so that a player's overall payoff is reduced by a factor  $mC_m$ , we see (Figure S2d) that mutations that increase memory eventually become worse invaders than mutations that decrease memory. In such cases an intermediate memory length evolves. Thus the evolution of memory depends on the costs associated with longer memories, as well as the size of the game being played. As we see in Figure S2a, shorter memories evolve, and much more slowly, when memory comes at a cost. Correspondingly (Figure S2b), the effect of evolving longer memories has a much weaker effect on the evolution of cooperation, although the general trend of reduced defection and increased cooperation is maintained.

## 7.7 Robustness and the dimension of strategy space

As discussed in the main text and shown in Figure 4, as memory increases the overall frequency of robust cooperators and defectors that evolve tends to decline. This reflects the fact that the absolute volume of robust strategies tends to decline as the dimension of strategy space increases - the probability of randomly drawing a strategy from the  $n$ -dimensional unit cube, that also lies within a robust volume with sides of fixed length, declines as a power of  $1/n$ . This decline in the robust volumes of strategies with the dimension of strategy space (both game size  $n$  and memory length  $m$ ) is shown in Figure S4.

## 8 Supplementary Figures

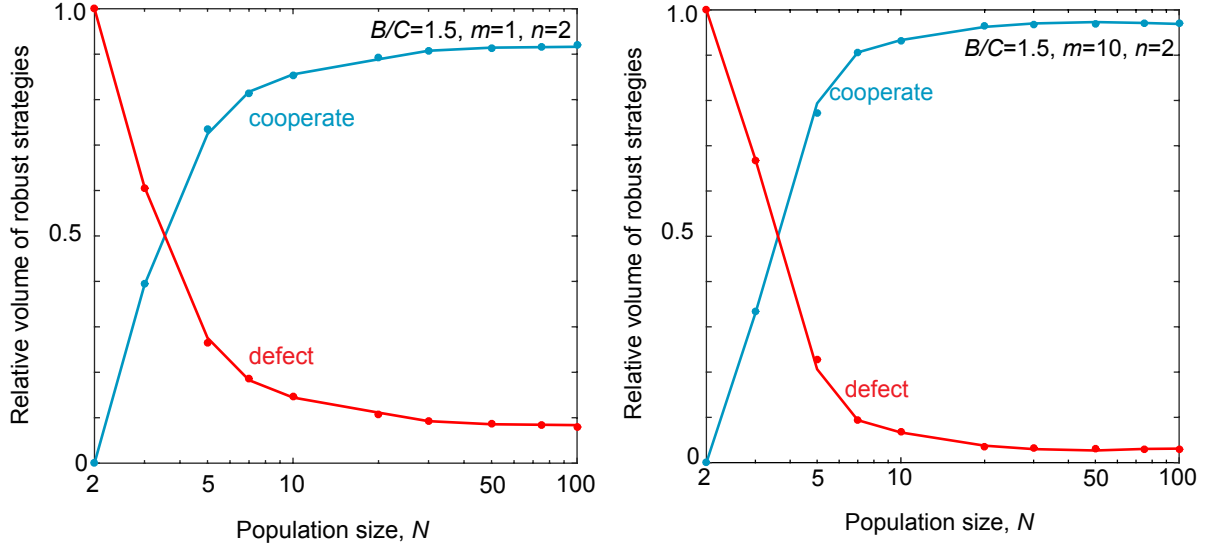


Figure S1: The impact of population size on cooperation. We calculated the relative volumes of robust cooperation – that is, the absolute volume of robust cooperative strategies divided by the total volume of robust cooperators and defectors – and compared this to the relative volume of defectors (solid lines) using Eqs. 2-3. We also verified these analytic results by randomly drawing  $10^6$  strategies and determining their success at resisting invasion from  $10^5$  random mutants (points). We calculated player's payoffs by simulating  $2 \times 10^3$  rounds of a public-goods game. We then plotted the relative volumes of robust cooperators and robust defectors as a function of populations size  $N$  with fixed game size  $n = 2$  and memory length  $m = 1$ , (left) and  $m = 10$  (right). In both cases the effect of increasing population size is to increase the relative volume of cooperators and decrease that of defectors. In all calculations and simulations we used cost  $C = 1$  and benefit  $B$  as indicated in the figure

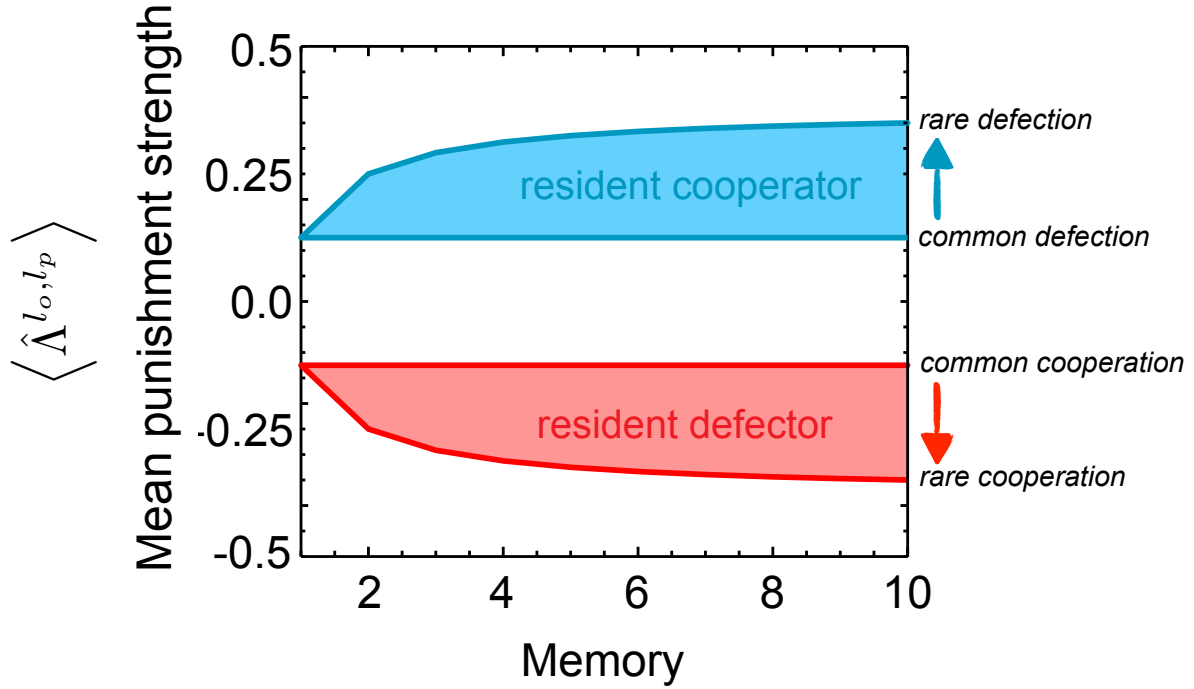


Figure S2: Effectiveness of contingent punishment. We calculated  $\frac{1}{(n-1) \times m} \sum_{l_o} \langle \hat{\Lambda}^{l_o, l_p} \rangle$  for the average punishment of a mutant who defected  $l_p$  times within the memory of the resident strategy, for both cooperators (blue) and defectors (red). As memory becomes longer, the average punishment increases for cooperators, making strategies more likely to be robust, and decreases for defectors, making strategies less likely to be robust.



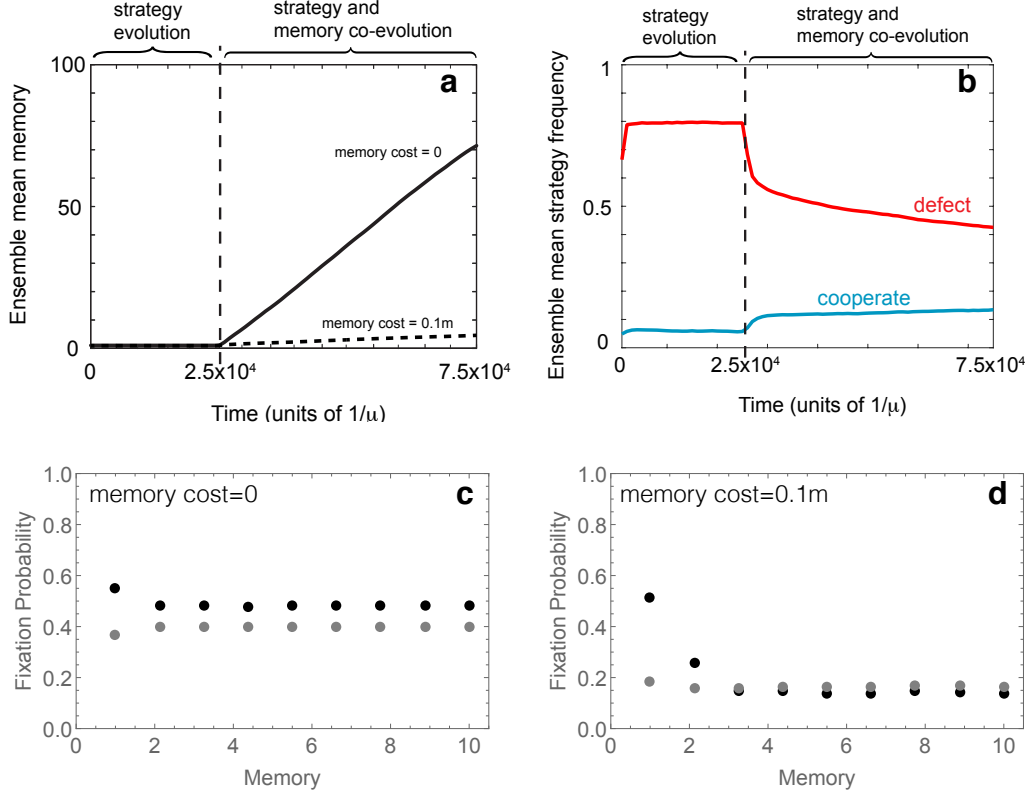


Figure S3: Invasibility of memory. We simulated co-evolution of memory and strategies as described in Figure 4 of the main text, with an additional cost to having memory which reduces a player's payoff by  $c_m \times m$ . We see that (a) much shorter memories evolve for  $c_m = 0.1$  compared to  $c_m = 0$  and (b) a correspondingly smaller amount of cooperation evolves. In order to understand why longer memory strategies evolve in small games we looked at the average fixation probability of mutations that increase or decrease memory, when played against a randomly drawn resident strategy. We drew  $10^6$  resident strategies for each memory length  $m \in \{1, 2, 3, \dots, 10\}$  and for each drew  $10^5$  mutants that increase memory length by 1 and  $10^5$  mutants that decrease memory length by 1. We assumed that a mutation that increased memory length by 1 did not change the probability  $p^{l_o, l_p}$  of the player's strategy. Where mutations increased memory length, we randomly drew probabilities  $p^{(n-1)(m+1), l_p}$  and  $p^{l_o, m+1}$ . (c) Plotted are the average fixation probabilities for mutations that increase (black dots) or decrease (gray dots) memory by 1. Each point shows the probability of in versus out transition for the state  $k$  (i.e mutations that result in increase in memory from  $k$  to  $k + 1$  and mutations that result in decrease in memory from  $k + 1$  to  $k$ ). When there is no cost to memory, mutations that increase memory length are always better invaders, for games of size  $n = 2$ . (d) When there is a cost to memory, mutations that decrease memory length do relatively better, and mutations that increase memory length do relatively worse. As a result we expect to see intermediate memory lengths evolve in the presence of costs.

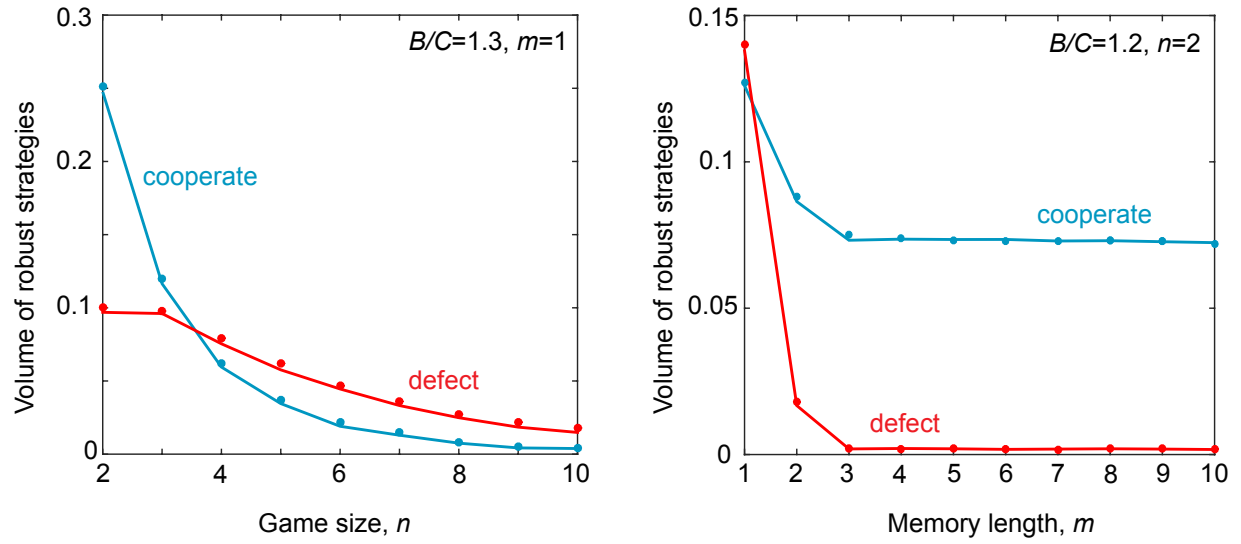


Figure S4: Absolute volumes of robust strategies. Here we show the same plot as in Figure 3 of the main text, using absolute rather than relative volumes. As is clear, the absolute volumes of both cooperators and defectors tends to decline as the dimension of strategy space increases. However this occurs at different rates for the different strategy types depending on whether game size (left) or memory (right) is increasing.

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